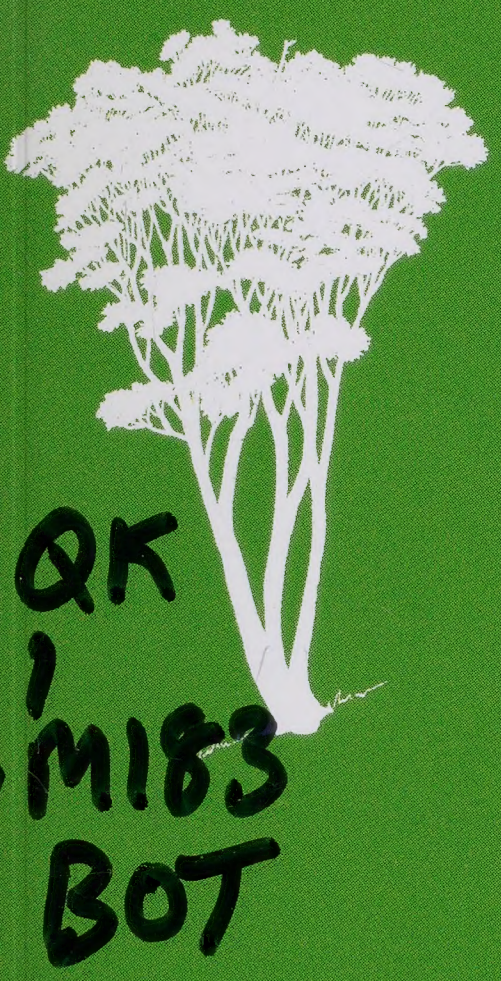

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NOTEWORTHY COLLECTION

CALIFORNIA

CARNEGIEA GIGANTEA (Engelm.) Britton & Rose (CACTACEAE). —Imperial Co., Palo Verde Mts., 3.6 km WNW of Palo Verde Peak and 0.4 km S of summit "1534T" on steep rocky ridge, single plant in desert scrub, SE ¼ of NE ¼ sec. 1, T10S, R20E, S.B.B.M., Palo Verde Peak USGS 7.5 min topographic quadrangle (1988, 2015), 33.334215°, –114.815776°, ca. 318 m, 2 June 2019, *Brett R. Goforth, PVM13* (RSA 882878).

Previous knowledge. *Carnegiea gigantea* is broadly distributed in the Sonoran Desert Floristic Province east of the Gulf of California, with northwestern range limits near the Colorado River boundary of California and Arizona (Britton and Rose 1920; Kearney and Peebles 1960; Shreve and Wiggins 1964; Turner et al. 1995). The range limits for *C. gigantea* at southeastern California are attributed to a climate gradient of reduced summer rainfall west of the Colorado River (Brum 1973; Steenbergh and Lowe 1977). This species has list 2B.2 status on the California Native Plant Society (CNPS) Inventory of Rare and Endangered Plants, and S1 state rank for being critically imperiled because of extreme rarity and vulnerability to extirpation (CNPS 2019). The California Natural Diversity Database (CNDDB) has recorded occurrences of *C. gigantea* on nine USGS 7.5 min topographic quadrangles at the Whipple Mts., Palo Verde Mts., and Chocolate Mts. (CNDDB 2019). These disjunctive occurrences are habitats with desert scrub vegetation at low elevations on rocky hillsides and outwash plains (Dawson 1966; Benson 1969; Munz 1974; McLaughlin et al. 1987; Anderson 2002; De Groot 2007; Ingram 2008).

There are apparently no previous collections of *C. gigantea* reported from the Palo Verde Mts. based on a search of the Consortium of California Herbaria database (CCH 2019) and the SEINet specimen network database (SEINet 2019). Two sightings reported >20 yr ago are recorded by CNDDB from the Palo Verde Peak 7.5 min quadrangle (CNDDB 2019). Each sighting was a single plant, mapped by CNDDB with position accuracy of 1.6 km at different locations (7.5 km apart): one plant was observed from aircraft on 14 June 1984 at a desert pavement near Flat Top, the other undated report was for occurrence at steep talus in the vicinity of Palo Verde Peak. The positions of both sightings are respectively 4.4 km NW and 3.9 km E from this collection. A checklist of vouchered plants for eastern Imperial County did not note any collection of *C. gigantea* at the Palo Verde Mts. (McLaughlin et al. 1987).

Significance. This is the first collection of *C. gigantea* to be reported from the Palo Verde Mts. for a new occurrence recorded in CNDDB. The nearest collections in California recorded by CCH are located at the Chocolate Mts. east of Mt. Barrow (SD 225698, 21 km SW), near Senator Wash north of Laguna Dam (POM 183663, 55 km SE), and the Whipple Mountains (e.g., JEPS 47152, 118 km NE). The nearest collection in Arizona reported by SEINet is 58 km SE at the Castle Dome Mountains (ASU 150455). Closer sightings in Arizona at the Colorado River Valley between Cibola (14 km E) and Ehrenberg (40 km NE) are noted on species range maps (Steenbergh and Lowe 1977; Turner et al. 1995).

A single plant was located on a ridge, rooted into rock fractures of weathered extrusive igneous rock at the base of an outcrop upslope (Fig. 1). The site had a NW aspect with 23° slope angle. Total height of the columnar stem (after Parfitt 2012) measured 4.91 m, with three short branches (30–45 cm long) at 2.9 m height on the trunk. A fourth branch bud at 1.7 m height was 7 cm long. All branches occurred on the

FIG. 1. View north of habitat and *C. gigantea* occurrence on 30 April 2019. Yellow tape measure at trunk is 1 m for scale. Photo credit: B. Goforth.

equator-facing side of the columnar stem. Stem diameter tapered at the trunk base, and was measured by caliper to be 40.7 cm at ground level, with narrowest diameter of 30.2 cm at 0.5 m height above ground level, 41.3 cm diameter at breast height (DBH, 1.4 m above ground level), and 44.0 cm at 2 m height.

At DBH, the columnar stem had three cavities. The cavity openings were 5 to 11 cm wide with circular to oval shapes, interconnected by excavated tunnels inside of the trunk. The pattern of trunk damage appeared similar to herbivory by *Neotoma albigula* Hartley (Hayes et al. 2013). Fecal pellets consistent with shape and size from *Neotoma* sp. were collected from inside the cavity. A midden located 2 m upslope from the plant contained chewed flower buds from the plant.

The plant was photographed on two dates in spring 2019 while in bloom to count flowers, buds, and fruit. On 30 April 2019, two branch tips and the columnar stem top had a total of 108 flower buds, nine open flowers, four closed browned flowers, and no fruit. Repeat survey on 2 June 2019 counted one flower bud, no open flowers, three closed browned flowers, and no fruit. This phenology was earlier and of shorter duration than noted elsewhere in the species range (e.g., Schmidt and Buchmann 1986).

The nearest weather station with a long-term record of rainfall is located 32 km N at Blythe, CA (119 m elev.). From 1946 to 2016, the mean annual rainfall was 90 mm with 34% of total in June–Sept. associated with the summer monsoon (WRCC 2016). The rainfall total at Blythe is 59% of the amount received at the Kofa Refuge in western Arizona where habitat is reportedly marginal for reproduction (Drezner 2008). Acknowledging uncertainties for the local amount of rainfall and runoff that influenced growth at the collection site, age-height relationships suggest this plant was between 90 and 120 yr old (Drezner 2003). This age range is consistent with observed branch and reproductive development (Drezner 2008, 2014a), as well as epidermal browning, scaling, and bark present on the trunk from ground level up to 1.3 m height on the equator-facing stem surface, and 1.1 m height on the poleward side (Evans and Fehling 1994; Evans et al. 2003).

Plant cover in the habitat was sparse, <20% total, with the land surface predominately barren rock outcrop and talus. Vegetation classified as the *Larrea tridentata* - *Ambrosia dumosa* Shrubland Alliance (Sawyer et al. 2009). Associated species included *Ambrosia dumosa* (A.Gray) Payne, *Aristida adscensionis* L., *Chaenactis carphoclinia* A.Gray var. *carphoclinia*, *Cryptantha angustifolia* (Torr.) Greene, *Encelia farinosa* A.Gray ex Torr., *Fagonia laevis* Standl., *Hoffmannseggia microphylla* Torr., *Larrea tridentata* (DC.) Coville, *Lepidium lasiocarpum* Nutt. subsp. *lasiocarpum*, *Phacelia crenulata* Torr. ex S.Watson, *Plantago ovata* Forssk. var. *fastigiata* (Morris) S.C.Meyers & A.Liston, and *Sphaeralcea ambigua* A.Gray.

Remoteness of this plant raises intriguing questions about the circumstances of establishment long ago. Occurrences of *C. gigantea* in marginal habitats are often associated with a "nurse-plant" or "nurse-rock" condition of shade which conserves moisture needed for establishment, such as under canopy cover of *Parkinsonia* sp. or below an outcrop (Brum 1973; Steenbergh and Lowe 1977; Hutto et al. 1986). The outcrop upslope likely provided a "nurse-rock" condition, but it is also possible that erosion of the steep slope may have removed a former "nurse-plant" because scattered *Parkinsonia florida* (Benth. ex A.Gray) S.Watson occurred on rocky hillsides nearby. The outcrop likely shed runoff which supplemented rainfall by concentration of water into fractures of the porous weathered rock where the plant rooted, to provide a "hydrologic refugia" (Drezner 2013; Winkler et al. 2018). Fruit of *C. gigantea* are consumed by many regional birds and mammals capable of dispersing seed to nurse sites at distant habitats (Drezner 2014b). Long-distance jump-dispersal of seed is expected to infrequently occur over lengthy periods of time (after Sauer 1988), and likely resulted in this rare occurrence.

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NOTEWORTHY COLLECTION

CALIFORNIA

CLINOPODIUM MENTHIFOLIUM (Host) Stace subsp. *ASCENDENS* (Jord.) Govaerts (LAMIACEAE). —Contra Costa Co., Temescal Creek Watershed, upper Claremont Canyon, Side-hill Trail, ~200 m W of Grizzly Peak Blvd.; 37.874732°, –122.224017°; 31 Jan 2021; chaparral on steep, south-facing slope; plants low, mounding subshrubs; a few dozen plants present, mostly past peak flower; flowers lavender-pink, leaves pleasantly aromatic; associated species include *Artemisia californica* Less., *Baccharis pilularis* DC., *Castilleja foliolosa* Hook. & Arn., *Chlorogalum pomeridianum* (DC.) Kunth, *Diplacus aurantiacus* (Curtis) Jeps., *Ehrharta erecta* Lam., *Eriophyllum confertiflorum* (DC.) A.Gray, *Lupinus albifrons* Benth., *Pinus* sp., and *Umbellularia californica* (Hook. & Arn.) Nutt.; inaturalist.org/observations/68899687; *Susan Fawcett and Bruce Baldwin 1418* (JEPS). Tilden Regional Park, Skyline Gardens, W end of Siesta Valley Recreation Area, along Skyline Trail; 2 miles E of Berkeley; 37.874209°, –122.219254°; 14 Feb 2021; chaparral restoration, with *Baccharis pilularis*, *Chlorogalum pomeridianum*, *Clinopodium douglasii* (Benth.) Kuntze, *Clinopodium vulgare* L., *Diplacus aurantiacus*, *Pentagramma triangularis* (Kaulf.) Yatsk., Windham & E.Wollenw., *Ribes californicum* Hook. & Arn. var. *californicum*, and *Toxicodendron diversilobum* (Torr. & A.Gray) Greene and growing in the vicinity; inaturalist.org/observations/69599303; *Susan Fawcett and Bruce Baldwin 1419* (JEPS). Tilden Regional Park, just W of Seaview Trail, along single-track following ridgeline; 37.886313°, –122.2232°; 15 Feb 2021; ridgeline grassland with Monterey pine overstory; large population, ~15 m × 6 m, high density, with many independent stems; associated species include *Artemisia douglasiana* Besser, *Chlorogalum pomeridianum*, *Clinopodium douglasii*, *Pinus radiata* D.Don, *Pseudognaphalium* sp., and *Rubus armeniacus* Focke; inaturalist.org/observations/69652828; *Susan Fawcett and Bruce Baldwin 1420* (JEPS). Tilden Regional Park, along Big Spring Trail, just below junction with Seaview Trail; 37.891051°, –122.227308°; 15 Feb 2021; annual grassland with scattered shrubs; associates include *Artemisia californica*, *Baccharis pilularis*, *Eriogonum nudum* Douglas ex Benth., *Geranium molle* L., *Lupinus albifrons*, and *Salvia leucophylla* Greene; plant a single mounding shrub in full flower, intermingled with *Salvia leucophylla* (out of its native range); inaturalist.org/observations/69652877; *Susan Fawcett and Bruce Baldwin 1421* (JEPS).

Previous knowledge. California is home to three native species of *Clinopodium*, *C. chandleri* (Brandegee) P.D.Cantino & Wagstaff, *C. douglasii*, and *C. mimuloides* (Benth.) Kuntze, and a fourth, *C. hortensis* Kuntze is in cultivation (Jepson Flora Project 2021). Of these, only *C. douglasii*, is native to the San Francisco Bay Area. An additional species, *C. vulgare* L. is recognized as an occasional escape in the East Bay hills (*Ertter 20919*, UC; *Ertter 21018*, JEPS; Ertter and Naumovich 2013) where it occurs in proximity to *C. menthifolium* subsp. *ascendens*, as at the Skyline Gardens locality (*Glen Schneider, Susan Fawcett & Bruce Baldwin s.n.*, JEPS). *Clinopodium menthifolium* subsp. *ascendens* may be distinguished from *C. douglasii* by its lavender to pink (vs. white) flowers, its suffrutescent (vs. creeping) habit, and its delicately textured (vs. thick and scabrous) leaves. It may be distinguished from *C. vulgare* by its elongate racemose inflorescence (vs. compact, rounded inflorescence) (Fig. 1).

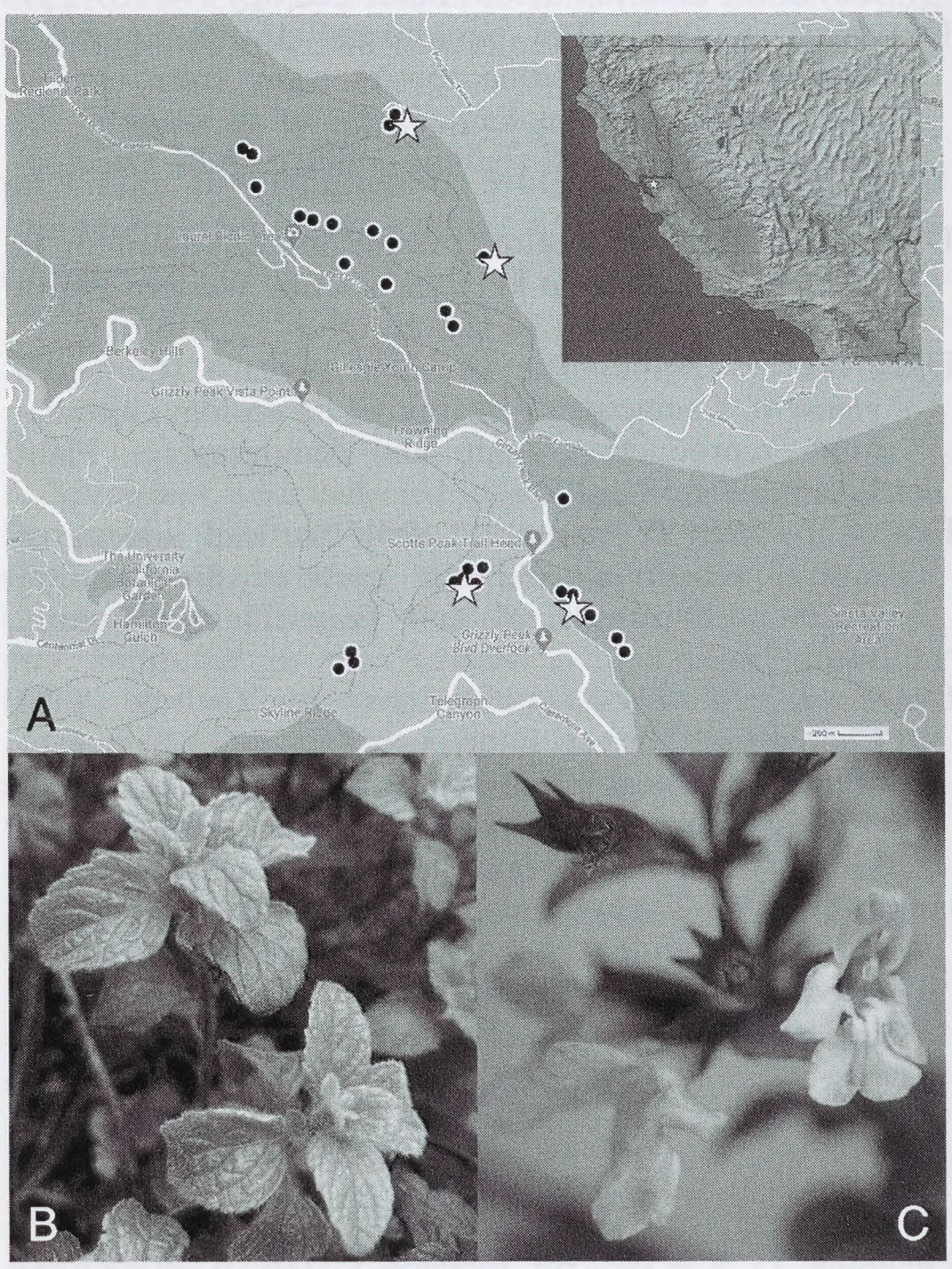

FIG. 1. A. Distribution map of *Clinopodium menthifolium* subsp. *ascendens* in the East Bay Hills, modified from iNaturalist. All occurrences were verified via ground-truthing, and all points are accurate to a minimum of 200 m. Circles correspond to iNaturalist observations, and stars indicate the herbarium vouchers cited here. B. The leaves of *C. menthifolium* subsp. *ascendens* are more delicate in texture and have longer hairs than those of *C. douglasii*. C. The flowers are generally pale lavender, and are borne in erect, elongate racemes. Photos by Susan Fawcett.

Clinopodium menthifolium is widespread in Europe, its native range extending across a broad climatic gradient, from the Mediterranean basin in the south, to Turkey and Ukraine in the east, and to the British Isles in the northwest, with *C. m.* subsp. *ascendens* occupying essentially the full species range (Tutin et al. 1972). *Clinopodium menthifolium* is considered introduced in British Columbia, Quebec, North Carolina and Connecticut (Kartesz 2015). It has had a complex taxonomic history, and in addition to its current disposition in *Clinopodium*, it has been treated in the genera *Satureja*, *Melissa*, and *Calamintha*, where it has combinations in five different species, though most of these are based on the basionym *Calamintha ascendens* Jord., with *Melissa intermedia* Baum. considered a heterotypic synonym.

The taxonomy of the Nepetoideae is in a state of flux, and additional data are needed before stability can be achieved, especially for New World taxa. The name *Clinopodium* has been broadly circumscribed to include more than 100 species, which is a conservative solution proposed by Cantino and Wagstaff (1998) pending finer resolution and increased sampling. However, in more recent molecular studies (e.g., Bräuchler et al. 2010) *Clinopodium menthifolium* subsp. *ascendens* resolves as a close relative of the type species of *Clinopodium*, *C. vulgare* (also native to the Mediterranean basin), and is likely to remain in *Clinopodium* s.s. This Old World clade is distantly related to native species of California currently recognized in *Clinopodium*.

The earliest collection of *Clinopodium menthifolium* subsp. *ascendens* in California that we have seen was made by Barbara Ertter (*Ertter 17518*, CDA, DAV, JEPS, RSA, UC) in 2000, in Strawberry Canyon, Alameda County, with later collections by her from the Vollmer Peak area in Contra Costa County (*Ertter 20918*, UC; *Ertter 21019*, JEPS). There are currently 44 observations of the taxon in California on iNaturalist (Fig. 1), in Siesta Valley Recreation Area, near the Strawberry Canyon Fire Trails and in Tilden Regional Park, spanning an area of approximately 4 km^2. The earliest of these was made by Kenichi Ueda in 2011 (inaturalist.org/observations/30086) in Tilden Regional Park. The plant is in cultivation nearby, on the University of California, Berkeley campus (inaturalist.org/observations/70122453). Additional records in Switzer Canyon, east of Balboa Park in San Diego County, and near Sea Ranch in Sonoma County need further verification.

Significance. The concern of the authors is that *Clinopodium menthifolium* subsp. *ascendens* is successfully established, sometimes at high densities, and is apparently spreading. It occurs in a diversity of largely intact native plant communities, and seems equally at home in sunny chaparral, oak woodland, non-native annual grassland, and under the shade of *Umbellularia californica*. As reviewed by Groves (2006), many invasive plant species undergo a lag phase, or period of latency, before spreading beyond reasonable efforts to control them. Despite recent advances in weed science, attempts to accurately predict potential 'sleeper weeds' has had limited success, and cannot keep pace with the ever-increasing number of introduced species (Dwyer 2008; Hulme 2012; Coutts et al. 2018). In observation of the precautionary principle, we recommend the eradication of the known East Bay Hills populations, all of which are on public lands managed for both recreation and conservation, rather than allowing the continued spread of a plant that has demonstrated its capacity to invade native habitats. Because of its limited extent and ongoing restoration efforts supported by a community of dedicated volunteers, controlling this plant is currently an achievable goal.

We would also like to highlight the utility of iNaturalist for monitoring plant populations. Herbarium specimens will remain a universal standard for the permanent documentation of plant diversity, and are an irreplaceable source of historical, morphological, and molecular data. We believe that iNaturalist complements herbarium specimen data, and has a number of advantages including: 1) large quantities of data may be rapidly collected and shared; 2) all data are immediately free and accessible to anyone with a smartphone or internet connection; 3) observations can be tracked in real time; 4) photos often provide useful context, including habitat and associated species; 5) many species can be identified using photographs; 6) locality data, including date, time, and GPS coordinates are collected automatically; and 7) the format allows for direct communication with observers (e.g., for the clarification of an occurrence as wild or under cultivation). We encourage readers to contribute their observations through iNaturalist, which, along with other citizen science platforms, has proven to be a rich source of data for research, education, conservation, and resource management (McKinley et al. 2017) and especially for the identification and monitoring of non-native plants (Sullivan et al. 2019).

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MADROÑO, Vol. 68, No. 2, pp. 67–68, 2021

NOTEWORTHY COLLECTION

CALIFORNIA

CYRTOMIUM FALCATUM (L.f.) C.Presl (DRYOPTERIDACEAE). —Santa Barbara Co., northwestern Santa Cruz Island, channel side, in Painted Cave, scattered patches in wet fissures on vertical and overhanging volcanic rock faces, ca. 15–30 m above the waterline, 34.0702, –119.8605, 19 September 2020, *C. M. Guilliams & K. Hasenstab-Lehman 6304* (SBBG).

Previous knowledge. *Cyrtomium falcatum* is a perennial, evergreen fern with erect, scaly rhizomes (Fig. 1). Leaves are 1-pinnately compound, with dark green pinnae usually in 4–10 pairs. Pinnae are distinctive in being relatively large (usually 8–12 cm long), often curved toward the leaf apex, and with oblique bases. Sori are scattered between the midrib and margin of the pinna; indusia are peltate. Three cytotypes of this species have been identified, two of which are sexually reproducing (a diploid and a tetraploid) and the other an apogamous triploid (Zhang and Barrington 2003).

Cyrtomium falcatum is native to east Asia and the Polynesian Islands, where it occurs in coastal and lowland forests to ca. 500 m (Zhang and Barrington 2003). This attractive species is widely cultivated as an ornamental, and has escaped and become naturalized in Europe, Hawaii, North America, South Africa, Réunion, Australia, and New Zealand. Occurrence records suggest that it may also be naturalized in the Azores, Madeira, and the Canary Islands. In North America, the species occurs across the southeastern U.S., with scattered occurrences in California. All North American plants are reported to be of the apogamous triploid cytotype (Yatskievych 1993). Since only a single spore of this cytotype is required to establish a new plant, it may be expected to spread more easily than the sexually reproducing cytotypes.

Significance. This collection of *C. falcatum* is significant for two reasons. First, it is the first specimen-based record of this plant from the northern Channel Islands, and is only the third specimen-based record from the archipelago (CCH2 Portal 2020). The first two collections of *C. falcatum* are from different locations on San Clemente Island (*Fallon 89-07* [SD], *Shute 11-58* [SD]). All three collections from the Channel Islands are from natural settings in low, coastal areas away from centers of human activity. Furthermore, there are no horticultural plantings of *C. falcatum* on the Channel Islands, to our knowledge. For these reasons, it seems likely that at least the initial colonization events for each island were from plants growing in nearby mainland locations, either in gardens or from where they have become naturalized along the coast of central and southern California.

This collection is also significant in owing its existence to the community science application iNaturalist (iNaturalist 2020). Although unidentified ferns have been known to occur in Painted Cave on Santa Cruz Island, the first definitive observation of *C. falcatum* was made via the iNaturalist application by James Bailey (iNaturalist username silversea_starsong) on 12 April 2019. Two other subsequent iNaturalist observations were made by different users prior to our collecting trip. Because the distinctive *C. falcatum* is readily identified from images, these observation-based records provided strong motivation for our trip. In this way, observation-based records through community science platforms such as iNaturalist can facilitate and encourage targeted efforts to voucher specific plants of interest.

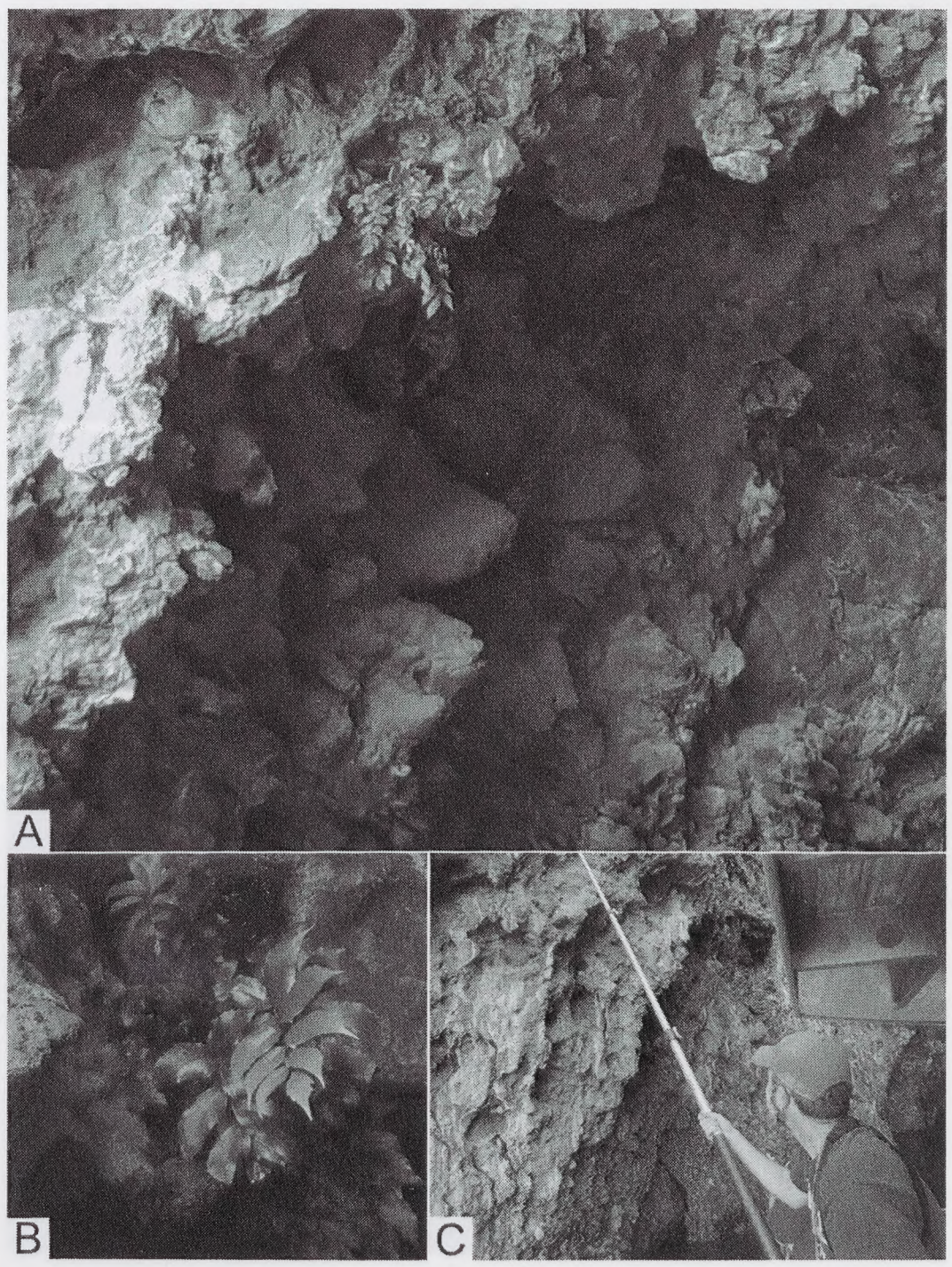

FIG. 1. *Cyrtomium falcatum* in Painted Cave, Santa Cruz Island, California. A. Cave wall, showing *C. falcatum* (photo by C.M. Guilliams); B. Close-up of *C. falcatum* (photo by James Bailey); C. Collector using a 24′ aluminum pole and collection device from boat deck (photo by K. Hasenstab-Lehman).

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NOTEWORTHY COLLECTION

CALIFORNIA

SPHENOPHOLIS INTERRUPTA (Buckley) Scribn. subsp. *CALIFORNICA* (Vasey) Scribn. (POACEAE). —San Diego Co., central Carlsbad, 492 m, location restricted by landowner; rare in two clay lens openings; 23 April 2020, *Margie Mulligan 3761* (SD) *with Jessie Vinje*; same locality, 9 May 2020, *Margie Mulligan 3762* (SD) *with Jon Rebman and Jessie Vinje*. Approximately 40 plants on one clay lens (Fig. 1) and several additional plants on another lens in chaparral with *Adolphia californica* S.Watson, *Comarostaphylis diversifolia* (Parry) Greene subsp. *diversifolia, Diplacus puniceus* Nutt., *Lonicera subspicata* Hook. & Arn. var. *denudata* Rehder, *Quercus dumosa* Nutt., *Rhus integrifolia* (Nutt.) Benth. & Hook. f. ex W.H.Brewer & S.Watson, and *Stipa lepida* Hitchc.. Clay lens associates include *Acanthomintha ilicifolia* (A.Gray) A.Gray, *Apiastrum angustifolium* Nutt., *Convolvulus simulans* L.M.Perry, *Deinandra fasciculata* (DC.) Greene, *Festuca microstachys* Nutt., *F. octoflora* Walter, *Hesperevax sparsiflora* (A.Gray) Greene var. *sparsiflora*, and *Sisyrinchium bellum* S.Watson. Nonnative species of concern include *Brachypodium distachyon* (L.) P.Beauv. and *Centaurea melitensis* L.

Previous knowledge. *Sphenopholis interrupta* subsp. *californica* (initially described as *Trisetum californicum* Vasey) was previously known from only two localities in the state of Baja California, Mexico and was last collected by Charles Orcutt at these locations in April 1886. San Diego Natural History Museum (SDNHM) surveys in 2017 and 2018 at the type locality determined that *Sphenopholis interrupta* subsp. *californica* was likely extinct. Orcutt collected the type (*Orcutt 1437*, lectotype US 868402!) on 19 April 1886 at "San Ramón" between Colonet and San Quintín in northwestern Baja California. A second collection (*Orcutt 1431,* W-Hackel 1916-0031884!) was previously made on 1 April 1886 from "Northern Baja California, near the U.S. boundary." Until recently, these were the only documented locations of this grass taxon. It should be noted that the other subspecies, *Sphenopholis interrupta* subsp. *interrupta* Scribn., is widely distributed in the western U.S. and northern Mexico but does not occur in California or Baja California (Rumely 2007).

Significance. The San Diego locality not only represents a rediscovery of a presumed extinct grass last collected by Orcutt in the late 1800s (Rebman et al. 2016), but also a new record for the USA, ca. 50 miles north of the estimated northernmost historical location. Recent botanical surveys at the type locality in Baja California failed to relocate this taxon because very little natural habitat remains for this species. Areas near the type locality are heavily impacted by agriculture and urban development, resulting in extreme habitat loss and fragmentation. Very little native habitat remains in the vicinity of the second Orcutt collection, "near the U.S. boundary," which is likely within present-day Tijuana.

The Jepson eFlora (Jepson Flora Project 2020) does not include this taxon because it was previously unknown from the USA and California. The species has been positioned in both *Trisetum* and *Sphenopholis* (Lamson-Scribner 1906; Finot et al. 2004) and does not key well in the Flora of North America (FNA) Poaceae keys where it is treated under *Trisetum* (Rumely 1993). This subspecies is not recognized in the FNA treatment because this publication only includes taxa north of Mexico. Rebman compared the Carlsbad sample to specimens of *S. interrupta* from Arizona and Texas and found significant differences including much heavier pubescence and shorter glumes and spikelets. Additional taxonomic research could determine if this taxon should be elevated to the species level.

Additional comments. Subsequent surveys of the remaining clay lens habitats near the coast in western

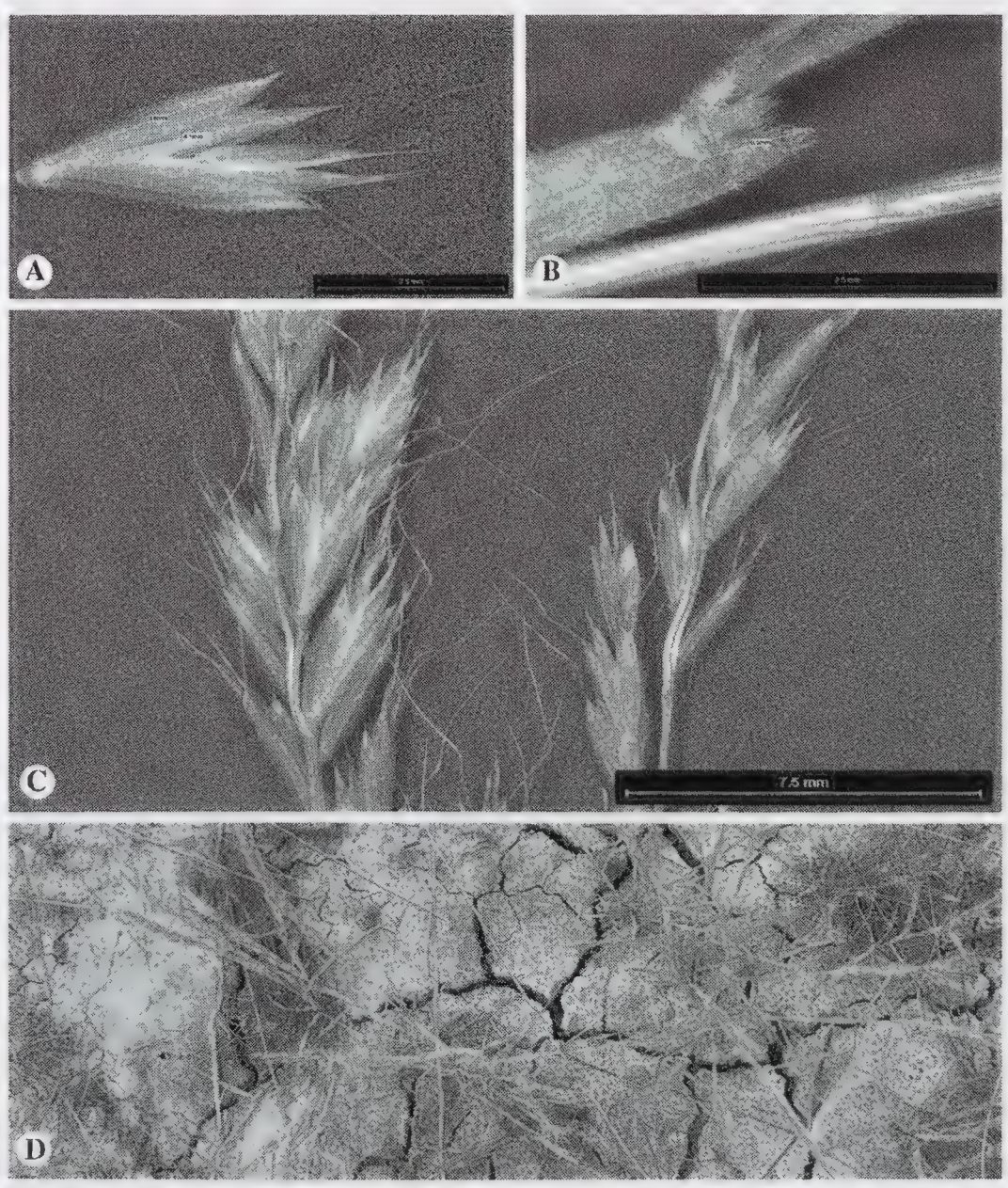

FIG. 1. *Sphenopholis interrupta* subsp. *californica* from Carlsbad, California. A. Close-up of spikelet (photo by J. Rebman); B. Part of leaf showing ligule and sheath (photo by J. Rebman); C. Inflorescence showing spikelets (photo by J. Rebman); D. Field shot of plants in clay lens with gray friable soils (photo by M. Mulligan)

San Diego County and northwestern Baja California could determine if additional populations exist. However, few clay lens habitats remain in San Diego County, with most dominated by nonnative and often invasive species such as *Brachypodium distachyon* that outcompete most native annuals.

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NOTEWORTHY COLLECTION

IDAHO

BOTRYCHIUM HESPERIUM (Maxon & R.T.Clausen) W.H.Wagner & Lellinger (OPHIOGLOSSACEAE). —Boundary Co., Kaniksu National Forest, Selkirk Mountains, Bog Creek Road off of Forest Service Road 1013, below Kaniksu Mountain; 1291 m; 48.980684°, –116.903819°; old road bed with moss carpet and mixed conifer saplings with *Fragaria, Danthonia,* and *Antennaria*; plants dull grey green and glaucous, common stalk with red tinge, sporangia orange, sporangia absent from lower pinnae; about 100 individuals within 9.3 m^2, second sub population about 100 m NE on roadbed. 21 July 2020, *Harpo Faust 3552 with Whitney Griswold* (ID, MICH, WTU).

Previous knowledge. Botrychium hesperium is found in the Rocky Mountains from Alaska south to northern Arizona (Farrar 2011) and New Mexico (Legler 2011), and west to the Cascade Mountains of Washington (CPNWH 2020). Adjacent to Idaho, it has been documented from northeast Washington, western Montana, and southern British Columbia (CPNWH 2020). The species was reported for Idaho by Wagner and Wagner (1993); however, we were unable to locate specimens at MICH or elsewhere to verify their report. A specimen at ISC (*Farrar HE100719*), collected in 2010, gives a location of "Idaho, Priest Lake District." This specimen was sent by an unknown individual to D. Farrar for identification, and no detailed locality information was provided (D. Farrar, Iowa State Univ., personal communication). Because the Priest Lake District includes portions of the Kaniksu National Forest in adjacent Washington, the specimen may have been collected in Washington instead of Idaho, potentially at a known site near the Roosevelt Grove of Ancient Cedars about 2 km west of the Idaho state line. *Botrychium hesperium* is typically found in mesic, montane to subalpine meadows, forest openings, and roadsides, often in gravelly soil (Farrar 2011; Hitchcock and Cronquist 2018).

Significance. First definitive collection for the state of Idaho. Plants were found growing within the road prism along Bog Creek Road. This road was constructed sometime between 1934 and 1956, then gated in the late 1980's to protect grizzly bear habitat (USCBP 2020). The road is currently impassible to vehicles; however, U.S. Customs and Border Protection plans to conduct repair and maintenance of the road to re-open it for motorized, administrative access (USCBP 2020). Plants within the road prism might persist under light maintenance regimes (e.g., brushing), but would likely be extirpated if the road is graded. Further survey work is needed to determine if the Bog Creek Road population extends outside the road prism, and other populations of *B. hesperium* should be sought in the Idaho Panhandle.

DIPHASIASTRUM ALPINUM (L.) Holub (LYCOPODIACEAE). —Boundary Co., Kaniksu National Forest: along FS Road 2624 ca 0.45 km NE of junction with Twenty Mile Road at Twenty Mile Pass; 1325 m; 48.566394°, –116.250817°; moist, shaded, mossy soil on edge of road bed, under *Thuja plicata* and *Tsuga heterophylla* Sarg. forest, with *Alnus sinuata* (Regel) Rybd., *Rubus pedatus* Banks & Sol. ex Lowe, *Cornus unalaschensis* Ledeb., *Tiarella trifoliata* L., *Lycopodium complanatum* L.; plants with long, creeping horizontal stems, leaves deep green, 4-ranked, dimorphic, several small patches of plants at edge of road bed; 29 June 2019; *Gab Raber 2019-13* (ID, WTU, MICH). Priest Lake State Forest, Selkirk Mountains, N of Lions Den campground off State Road 44, The Lions Head, pond directly below The Lions Head; 1968 m; 48.783001°, –116.718793°; small flat depression among boulders along pond in basin, organic soil with *Carex* carpet with *Phyllodoce* and small *Abies* saplings, plants blue-green with 4-ranked, dimorphic leaves, single small patch around 30 cm across, at edge of *Abies* saplings; 16 August 2019; *Harpo Faust 2019-1862 with Ben Legler* (ID). Priest Lake State Forest, Selkirk Mountains, N of Lions Den campground off State Rd 44, The Lions Head, ca 500 ft E of East Lions Head Peak; 2044 m; 48.786456°, –116.713862°; heath meadow dominated by *Phyllodoce* and *Cassiope* with young *Abies* at edge adjacent to granite boulder slope, several clumps within 3 m area, spreading among *Cassiope* and *Phyllodoce*; foliage blue green, leaves 4-ranked and dimorphic; 16 August 2019; *Harpo Faust 2019-1888 with Ben Legler* (ID, MICH).

Previous knowledge. Diphasiastrum alpinum is a circumboreally distributed species extending south through western Canada to Washington and northwest Montana (Wagner and Beitel 1993; CPNWH 2020). It has been previously reported from northern Idaho by Lellinger (1985) and Wagner and Beitel (1993), neither of whom cited voucher specimens or other verifiable records. Sadly, the authors for the Flora of North America treatment for this group are both deceased. Searches of online specimen data portals turned up no prior specimens from Idaho to verify their reports. We then contacted staff at MICH and NY, where Wagner and Beitel were based, respectively. Staff of the MICH herbarium familiar with their work were able to locate a specimen in their backlog (*Shaw 1044*, MICH

1571109) that may be the sole basis for Wagner and Beitel's (1993) report of *D. alpinum* from Idaho (Richard Rabeler, Univ. of Michigan, personal communication). Affixed to this specimen is a typed copy of the collector's original label that interprets the locality as "Idaho (?), Fremont County (?), alpine meadow in the Big Bend district." The attribution of the specimen to Fremont County, Idaho, is incorrect. The specimen is part of the Charles Shaw Selkirk Flora collection from the early 1900's, all of which were collected in the British Columbia, Canada portion of the Selkirk Range (PCC 2020). Four duplicate specimens of *Shaw 1044* were then located at NY; all four are correctly attributed to British Columbia.

Significance. The specimens cited here verify the presence of *D. alpinum* in Idaho. The 2019 collections made in the Selkirk and Purcell mountains of northern Idaho fill a gap in the known distribution as they are all under 80 kilometers from the closest collections in Montana and British Columbia. Two of the three collections cited here were found in open, subalpine meadows, growing inconspicuously amidst *Cassiope* and *Phyllodoce*. The other collection was made on a roadside at mid elevation. It is safe to presume there are more populations of this species in northern Idaho, and it should be sought in subalpine heath meadows and high elevation roadsides. *Diphasiastrum alpinum* is sometimes confused with *Diphasiastrum sitchense* (Rubr.) Holub, but is differentiated by its dimorphic, 4-ranked leaves (Wagner and Beitel 1993). Hybrids show intermediate morphological characters and are occasionally found where the two parent species co-occur (e.g., in the Cascades of Washington, CPNWH 2020). Two hybrid specimens are known from northern Idaho (CPNWH 2020).

ELYMUS HIRSUTUS J.Presl (POACEAE). — Boundary Co., Kaniksu National Forest, Selkirk Mountains, 0.9 mile SE of Hidden Lake on West Fork Lake Trail; 1502 m; 48.87259°, –116.748027°; mossy trail side drainage dominated by ferns, *Alnus*, *Rhododendron*, *Vaccinium*, *Senecio* with 100 yr old *Picea* and *Abies* forest surrounding; 25 July2019; *Harpo Faust 2019-1490 with Peri Lee Pipkin, Beau Romeo* (ID, UTC). Kaniksu National Forest, Selkirk Mountains, Smith Creek Road, Forest Service Road 281, Smith Creek; 1315 m; 48.841314°, –116.704086°; disturbed old logging site with grass covering of *Elymus, Calamagrostis, Phleum* with *Rubus nutkanus* Moc. ex Ser., *Heracleum maximum* W.Bartram, *Acer glabrum* Torr., and *Sambucus racemosa* A.Gray; abundant population of 500 individuals in 1 acre; 15 July 2020; *Harpo Faust 3434 with Whitney Griswold & Ben Legler* (ID, NYBG, UBC). Kaniksu National Forest, Selkirk Mountains, Smith Creek Road, Forest Service Road 281, Smith Creek; 1192 m; 48.873263°, –116.71837°; natural opening within conifer forest disturbed by logging activity, very moist with *Heracleum, Senecio, Salix,* and *Calamagrostis*, 15 July 2020; *Harpo Faust 3458 with Whitney Griswold & Ben Legler* (ID, MONTU, WTU). Kaniksu National Forest, Selkirk Mountains, Smith Creek Road, Forest Service Road 281, Smith Creek; 1161 m; 48.881255°N, –116.714782°W; open *Thuja plicata* Donn ex D.Don old growth adjacent to stream with high brushy layer of *Athryium felix-femina* (L.) Roth, *Aconitum columbianum* Nutt., and *Heracleum maximum*; 15 July 2020; *Harpo Faust 3467 with Whitney Griswold & Ben Legler* (ID).

Previous knowledge. Elymus hirsutus was previously known from coastal mountains in Alaska, British Columbia, and Washington, extending sporadically inland to eastern British Columbia, and grows in environments ranging from moist to dry thickets, woodlands, and grasslands (Barkworth et al. 2007). It is similar in habit to *Elymus glaucus* Regel, but has pendant spikes and 0.5–1 mm long hairs on the lemma margins (Hitchcock and Cronquist 2018).

Significance. First reports for Idaho. These collections extend the known distribution southwards by about 100 km from the nearest populations in southeastern British Columbia (CPNWH 2020). The 2019 collection was found in a moist trailside drainage near a tributary to Smith Creek. Three additional collections were obtained from other locations along Smith Creek during follow-up surveys in 2020. Additional populations of *Elymus hirsutus* should be expected in the Idaho Panhandle, and *Elymus glaucus* collections found in mid elevation moist forests warrant review.

Euphrasia nemorosa *(Pers.) Wallr. (OROBANCHACEAE)*. Bonner Co., Kaniksu National Forest, Selkirk Mountains, Priest Lake Ranger District, Forest Service Road 1013, Upper Priest RNA, Navigation Trail 291; 816 m; 48.81298°, –116.954122°; weedy trailside with peat carpet amidst disturbed *Pinus monticola* Douglas ex D.Don dominated forest with *Hypericum, Medicago,* and *Fragaria*; flowers white, axillary, plants found scattered in trail; 9 August 2020; *Harpo Faust 3803 with Whitney Griswold* (ID). Boundary Co., Priest Lake State Forest, Selkirk Mountains, Dodge Creek Road, beyond first gated road about 0.5 mile, first left on unnamed road; 841 m; 48.54489°N, –116.478028°; moist old road bed amidst logged mixed conifer forest with gravelly soil, road bed covered in *Leucanthemum vulgare* Lam., *Hypericum perforatum* L., *Trifolium arvense* L.; corolla white with upper 2 petals light purple with yellow splotch, plants branching, abundant and matting road; 10 Aug 2020; *Harpo Faust 3825 with Whitney Griswold* (ID, NYBG, WTU).

Previous knowledge. Euphrasia nemorosa is a hemiparasitic annual species native to Europe and established in eastern and western North America (Gussarova 2019). Earlier workers treated North

American populations of this species broadly under the ambiguous name *E. officinalis* L. (Hitchcock and Cronquist 1973; Gleason and Cronquist 1991) or as multiple, narrowly defined species, both native and introduced (Fernald and Weigand 1915). Disagreement remains over whether North American populations of *E. nemorosa* are native (Kartesz 2015; MNFI 2020), introduced (Gussarova 2019), or both (NatureServe 2020). In western North America, *E. nemorosa* is generally regarded as introduced (Douglas et al. 1999; Jaster et al. 2017; Hitchcock and Cronquist 2018) and occurs from Alaska south to northwest Oregon, mostly west of the Cascade and Coastal mountains, with additional populations established in eastern British Columbia, northeast Washington, and northwest Montana (CPNWH 2020). Plants usually occur in moist to dry, often gravelly, ditches, fields, and roadsides (Hitchcock and Cronquist 2018).

Significance. First collections for Idaho. With nearby collections surrounding the Idaho Panhandle, this collection fills a gap within the greater distribution of *E. nemorosa*, and the species should be expected elsewhere in the state.

UTRICULARIA OCHROLEUCA R.W.Hartm. (LENTIBULARIACEAE). —Bonner Co., N shore of Priest Lake, Mosquito Bay, on private land; 2443 ft; T62N R04W S10 NW1/4, 48.74397°, –116.84355°; large open bog with a few raised "islands" of *Pinus contorta*, vegetation dominated by patches of *Carex livida* Willd., *Carex lasiocarpa* Ehrh., *Carex rostrata* Stokes, *Dulichium arundinaceum* (L.) Britton, *Eriophorum chamissonis* C.A.Mey., *Potentilla palustris* (L.) Scop., *Spiraea douglasii* Hook., and *Andromeda polifolia* L., with *Kalmia microphylla* (Hook.) A.Heller in spots over moist to saturated *Sphagnum* mat; common, submerged macrophyte in water less than 10 cm deep with much detritus, flowers bright yellow, emergent, water pH 4.5, bladders both on leaves and on specialized branches; 17 June 1987; *R. Bursik 114* (ID). Panhandle National Forest, Kaniksu Marsh RNA, ca. 8 mi S of Priest Lake; 2480 ft; T59N R4E S25 NW1/4, 48.440363°, –116.920234°; large open *Sphagnum* fen dominated by *Carex lasiocarpa*, *C. rostrata*, *Dulichium arundinaceum*, and *Scirpus acutus* Muhl. ex Bigelow surrounded by a shallow moat (0.1 to >1 m deep), which is dominated by *Brasenia schreberi* J.F.Gmel., *Nuphar polysepala* Engelm., and *Potamogeton natans* L.; water chemistries: total hardness 10 mg/liter, Ca 2.72 mg/liter, Mg 0.78 mg/liter, substrate pH 5.5; common in pools to 1 m deep, formed in holes throughout the floating mat; 5 July 1987. *R. Bursik 332* (ID); Priest Lake RD ca. 0.5 mi N of Priest Lake Service Station, Lamb Cr. Meadows off Hwy 57, pvt/USFS land; 2567 ft; T35N R5W S23 SW1/4; 48.532253°, –116.943406°; open, ditched fen dominated by *Carex lasiocarpa*, *C. utriculata* Boott, *C. lanuginose* Michx., *C. buxbaumii* Wahlenb. in patches, shallow standing water throughout, no moss cover, rare in water channels to 6 inches deep; 14 June 1991; *R. Bursik 1701* (ID). Kaniksu March, ca. 1 mi S of Dickensheet Junction, T59N R4W S30 NW1/4; 48.440371°, –116.912942°; plants floating in small pools amid *Sphagnum* mats; August 2000; *Curtis R. Bjork s.n. & Robin O'Quinn* (ID); Priest Lake State Forest, base of Selkirk Mountains, 1.5 mi N of Indian Creek Unit, Bear Creek Basin; open *Sphagnum* bog with standing water, *Pinus monticola* saplings, associated species: *Drosera*, *Betula*, and *Carex*; ca 50 individuals in flower in 1 acre area; 725 m; 48.631808°, –116.836634°; 12 September 2019; *Harpo Faust 2019-2057 with Ben Legler* (ID, NYBG).

Previous knowledge. *Utricularia ochroleuca* is known from scattered locations in western North America extending from the Yukon south to Montana, Washington, Oregon, and California (Ceska and Bell 1971; Baldwin et al. 2012; CPNWH 2020). With a circumboreal distribution, it is also found across Europe, with the type specimen locality in Sweden (Hartman 1857; GBIF 2020). It is likely more abundant than currently reported, as it is easily confused with both *Utricularia intermedia* L.Vaill. and *Utricularia minor* Thuill. and may be of hybrid origin between the two species (Ceska and Bell 1971).

Significance. First reports for Idaho. Following discovery of the 2019 collection, all Idaho collections of *Utricularia intermedia* and *Utricularia minor* at ID were reviewed and four earlier collections were located and annotated. Additional populations of *U. ochroleuca* should be sought in other fen systems throughout Idaho.

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CORALLORHIZA MACULATA (ORCHIDACEAE) NEW TO ALASKA AND ITS DISTRIBUTIONAL RELATIONSHIP TO *CORALLORHIZA MERTENSIANA*

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ABSTRACT

In the Pacific Northwest, the spotted coralroot, *Corallorhiza maculata* (Raf.) Raf., has been recognized as occurring as far north as central British Columbia, but excluded from the flora of Alaska. The western coralroot, *C. mertensiana* Bong., reaches its northern range limit in Southeast Alaska, where collections of this sister species may be confused with *C. maculata*. In 2019-20, we conducted herbarium and field studies that verified eight *C. maculata* stations in northern Southeast Alaska. Two of these stations are represented by collections made in 2000 and 2007, which were identified as *C. mertensiana*; 14 *C. mertensiana* collections had been identified as *C. maculata*. This confusion may have resulted from nomenclatural changes, as well as rarity of actual *C. maculata* material. These species differ in morphological features that reflect different breeding systems, and occupy different habitats in Alaska. The Alaska stations of *C. maculata* represent a 650 km range extension that is disjunct from locations in central British Columbia. These stations occur in a summer-dry climate zone caused by a rainshadow from coastal mountains. We advance the hypothesis that this area provides habitat for populations of *C. maculata* that represent relics of a floristic migration that occurred during the Xerothermic interval 10-7500 yr BP. In contrast, *C. mertensiana* is widespread in humid coastal habitats in southeast Alaska, and its distribution is contiguous with more southern coastal populations. Though both species occur in Southeast Alaska, they occupy different climate zones, and their distributions are narrowly allopatric.

Key Words: Alaska, climate relic, *Corallorhiza maculata, Corallorhiza mertensiana*, field and herbarium records, morphology, migration, rain shadow, Xerothermic Hypsithermic interval.

Two species of coralroot (Orchidaceae), *Corallorhiza mertensiana* Bong. and *C. trifida* Châtel, have been attributed to Alaska (USA) by state (Anderson 1959; Hultén 1968, Welsh 1974); regional (e.g., Brown and Folsom 2006), and North American (Correll 1950; Luer 1975; Freudenstein 1997; Magrath and Freudenstein 2002) treatments. Nomenclature follows Flora of North America Editorial Committee (1993), except as referenced. *Corallorhiza trifida* is widespread in Alaska, but *C. mertensiana* occurs only in Southeast Alaska. A third coralroot species, *C. maculata* (Raf.) Raf., was reported from Alaska as *C. multiflora* Nutt. by Rydberg (1917), but there appear to be no supportive specimens. This species has been recorded from British Columbia, Canada, primarily to the south of Southeast Alaska (Correll 1950; Luer 1975; Freudenstein 1997; Magrath and Freudenstein 2002). Several outlier collections are also mapped from northern BC by Szczawinski (1959) and Douglas et al. (2002).

After finding *C. maculata* var. *maculata* in Southeast Alaska in 2019, we sought to determine whether other stations occur in Alaska and to compare their distribution with those of the superficially similar *C. mertensiana*, which is widespread in Southeast Alaska. We also asked whether this taxon might be represented in herbaria by Alaska specimens that were overlooked or identified as *C. mertensiana*. In this study, we review the identities of *C. maculata* and *C. mertensiana* specimens at the University of Alaska Museum of the North Herbarium (ALA) accessed through ARCTOS (2019), as well as four regional herbaria. We provide habitat and soil descriptions of extant *C. maculata* populations and contrast them with those of *C. mertensiana*. We also compare regional climatic characteristics for these species and use this information to develop a hypothesis for the origin of *C. maculata* in Alaska.

Study Area

Southeast Alaska represents the northern-most extension of coastal rainforest of the Pacific Western States. Its 800 km coastline includes the Alexander Archipelago island chain, as well as adjacent mountains that reach over 2500 m above sea level. The climate of this region is primarily wet maritime, averaging over 300 cm annual precipitation. However, some areas may come under the influence of continental climate, resulting in warmer summers

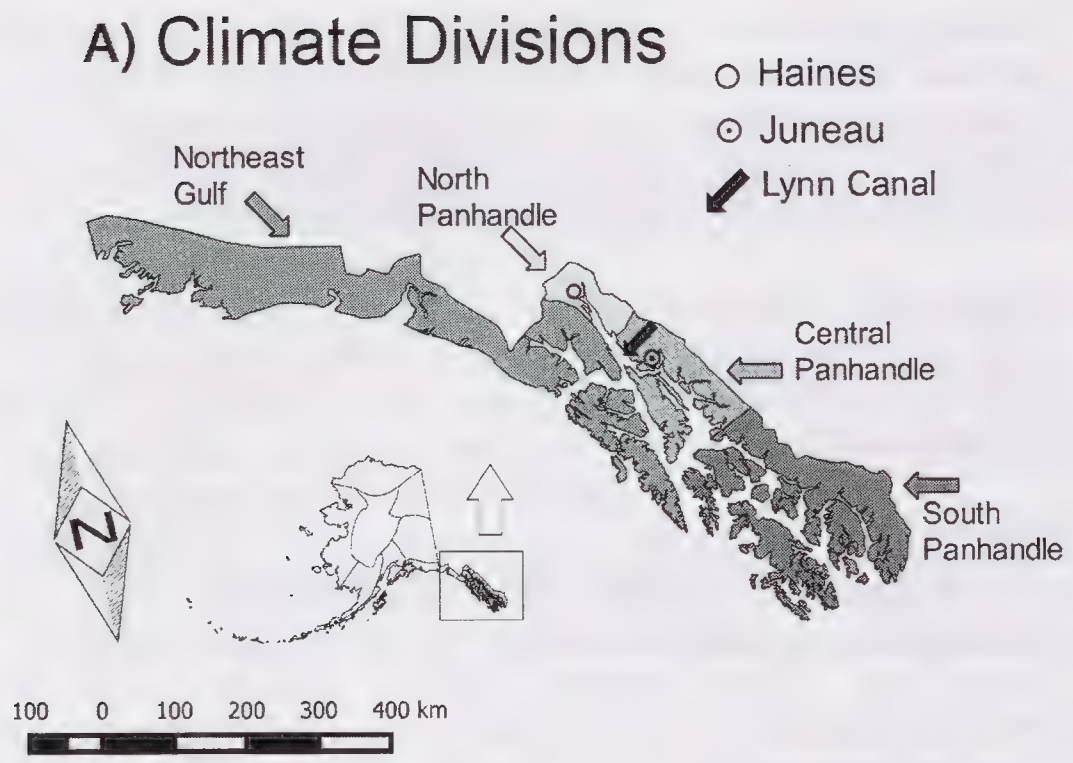

FIG. 1. Climatic characteristics of Southeast Alaska. A) climate divisions of Southeast Alaska from Bieniek et al. (2012). B) Average (+SE) growing season precipitation and temperature for North Panhandle, Central Panhandle and Northeast Gulf Climate Divisions. Kruskal-Wallis one-way ANOVA: Temperature ($\chi^2 = 24.361$, $P < 0.001$; Precipitation ($\chi^2 = 103.898$, $P < 0.001$). All values are significantly different between climate divisions with the Kruskal-Wallis Multiple-Comparison Z-Value Test. See Appendix 1 for seasonal differences.

and colder winters. Of special interest is the extreme north reach of the Lynn Canal fjord and its major tributaries, which penetrate coastal mountains and lie in the North Panhandle Climate Division (Fig. 1). This area is climatically distinct from the rest of Southeast Alaska due to its warmer summer temperatures, lower precipitation and reduced evapotranspiration (Anderson 1955; Patric and Black 1968; Bieniek et al. 2012). These differences result from a rain shadow effect caused by an extension of the Chilkat Range of the St. Elias Mountains adjacent to the west (Anderson 1955; Bieniek et al. 2012). As a result of its climate and location, upper Lynn Canal serves as a species-rich contact zone supporting both coastal and interior continental vegetation, and contains about 60% more species than other coastal zone geographic areas (Hultén 1968; Farr and Hard 1987; Hall 1995; Alaback 1996; Parker 2001).

Climate and post-glacial migration strongly affect vegetation composition in Southeast Alaska and adjacent British Columbia (Andersen 1955; Mathewes 1985). The predominant coastal vegetation is northern rainforest of *Picea sitchensis* (Bong.) Carrière and *Tsuga heterophylla* (Raf.) Sarg., or muskeg peatland with *Pinus contorta* Dougl. ex Loud. var. *contorta* and *Tsuga mertensiana* (Bong.) Carrière (Heusser 1960). *Populus trichocarpa* Torr. & A.Gray ex Hook., *P. contorta* var. *latifolia* Engelm. and *Betula papyrifera* Marshall tend to occur in drier habitats with continental climates, especially after disturbances such as fire. *Thuja plicata* Donn ex D.Don and *Chamaecyparis nootkatensis* (D.Don) Spach occur in lowland forests and muskeg of southern southeast Alaska. Southeast Alaska soils are primarily acidic and developed in organic matter from partially decomposed plant material of forests or peatlands. They vary in depth to bedrock or glacial material and are often complex due to wide variation in underlying bedrock.

Study Species

The identities of plants referred to as *C. mertensiana* and *C. maculata* in southeast Alaska have been uncertain (e.g., Hultén 1941; Hall 1995). Although *Corallorhiza mertensiana* had been treated as a distinct species by Correll (1950), Calder and Taylor (1965) treated it as *C. maculata* (Raf.) Raf. subsp. *mertensiana* (Bong.) Calder and Taylor. They suggested that lip characteristics previously used to separate these species were not always reliable, but used other diagnostic floral features to separate these taxa (Calder and Taylor 1968). However, Luer (1975) used these features to recognize *C. mertensiana* at the species level.

Based on morphological and molecular data, *C. maculata* and *C. mertensiana* have been resolved as sister species within the *C. maculata* clade (Freudenstein 1994, 1997). They differ in distribution, breeding system, and floral morphology (e.g. Correll 1950; Freudenstein 1997; Fig. 2). Nevertheless, where their ranges overlap, they may intergrade (Magrath and Freudenstein 2002). *Corallorhiza maculata* occurs across much of North America, while *C. mertensiana* is restricted to the Pacific Northwest (Freudenstein 1997). *Corallorhiza maculata* exhibits facultative self-pollination through delayed autogamy (Catling 1983). It also has a reduced adnate mentum (a small nectar spur) and a less divergent perianth than *C. mertensiana*, which may reflect selection toward self-pollination, a key character of this species (Freudenstein 1997). The more divergent

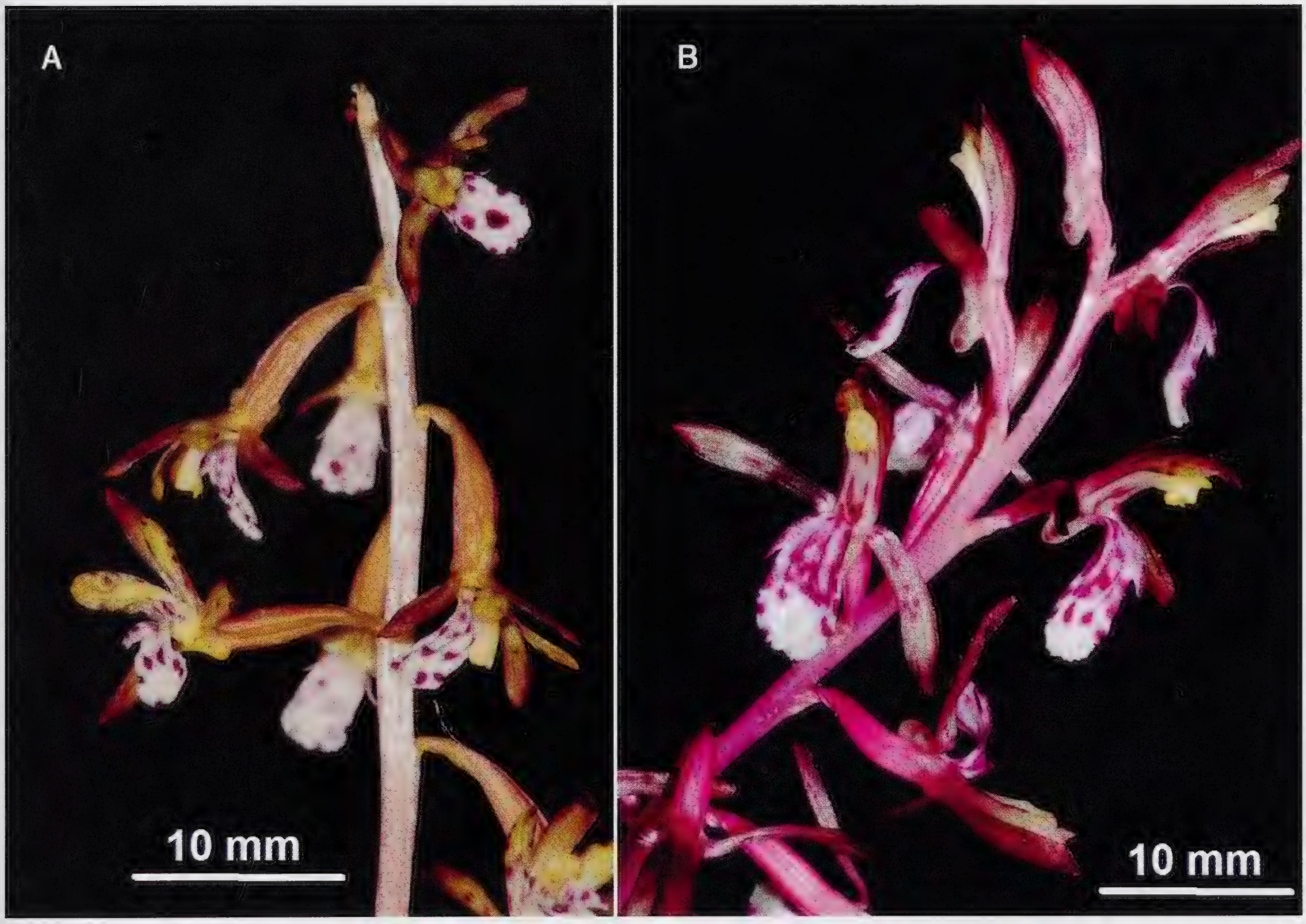

FIG. 2. Photographic comparison of A) *Corallorhiza maculata* var. *maculata,* and B) *C. mertensiana.* Photo sources: *C. maculata* (Station No. 3), *C. mertensiana,* Douglas Island, AK. Scale is approximate. Photos: M. L. Bowles.

and showy perianth, longer and more upright column, and saccate mentum of *C. mertensiana* suggest selection toward nectar-seeking pollinators and an outcrossing breeding system, and it has been observed to be bee-pollinated (M. L. Bowles and R. Armstrong unpublished data). *Corallorhiza maculata* flowers have a white lip with red-purple spots, and a stem that ranges from reddish to brownish to purplish. *Corallorhiza mertensiana* has a white lip with red-purple streaks or spots, or a pure red-purple lip; and a red-purple stem. Freudenstein (1997) recognized two varieties of *C. maculata*, which are widespread in North America. Variety *occidentalis* differs by an expanded middle lobe of the distal end of the labellum, larger floral bracts and more divergent perianth than var. *maculata*. Variety *occidentalis* also tends to flower earlier than var. *maculata* where they co-occur. Both species have forms with anthocyanin-free flowers and stems that appear as yellow plants with white lips.

METHODS

Climate

To elucidate climatic characteristics of *Corallorhiza maculata* and *C. mertensiana* habitats in northern Southeast Alaska, we statistically compared the 20-yr (2000-2019) average annual growing season (May-August) precipitation and temperature of the North Panhandle Climate Division with that of the Central Panhandle Climate Division and the Northeast Gulf Climate Division (Fig. 1). Following Bieniek et al. (2012) we made this comparison using data from Haines (North Panhandle), Juneau (Central Panhandle) and Elfin Cove and Sitka (Northeast Gulf). To focus on the portion of the Northeast Gulf bordering the North Panhandle, we excluded data from Cordova, Valdez and Yakutat. Data were accessed through NOAA-ACIS (2019). The Kruskal Wallis one-way ANOVA and Multiple Comparison Tests were used to test whether each climate division differed from the other divisions in temperature and precipitation. We also used these tests to make separate comparisons within spring (May-June) and summer (July-August) portions of the data set, and report multiple comparisons between climate divisions.

Herbarium Studies

We examined 58 *Corallorhiza maculata* and *C. mertensiana* specimens collected in Southeast Alaska to determine their identities and the prevalence of each species. Jpeg images of 41 specimens were accessed through ARCTOS (2019). We also exam-

ined images of two specimens each from the Glacier Bay National Park herbarium (GB), Gustavus, and the Klondike Goldrush National Historical Park herbarium (KLGO), Skagway. Seven physical specimens were examined at the U.S. Forest Service (USFS) Forestry Sciences Lab herbarium (FSL), Juneau, and six in the Juneau Botanical Club herbarium (JBCC) at the Alaska State Museum, Juneau. We also examined Orchidaceae specimen images provided from the USFS herbarium at Yakutat, but only *C. trifida* was in this collection.

The following characters were used to separate *C. maculata* and *C. mertensiana* specimens. *Corallorhiza maculata*: perianth minimally divergent; lip white with red-purple spots and with two basal lobes; mentum inconspicuous and adnate to the ovary; and column projecting forward, <6 mm long. *Corallorhiza mertensiana*: perianth broadly divergent; lip down-curving and red-purple to white with red-purple streaks or spots and often with a pair of lateral teeth; mentum conspicuous and free at the distal end, with this character persisting in fruiting specimens; column upright, 6–8 mm long. Because the mentum tends to persist during fruit development, its structure is important in separating these species; however, specimens in an advanced stage of fruit formation may not be separable.

Field Studies

To assess the presence of extant populations of *C. maculata*, we conducted field surveys of road- and trail-accessible potential habitats in the initial discovery area, and in the vicinities of the locations of two correctly identified herbarium specimens (Table 1). This included a corridor along the Chilkat River extending north and south from Haines, AK, and the Taiya Inlet area of upper Lynn Canal near Skagway, AK. These areas lie within the North Panhandle Climate Division. Within these areas, we were able to access sites ranging in altitude from near sea level to lower mountain slopes. Voucher collections were made from newly discovered *C. maculata* stations when multiple plants were present. When single plants were present, their occurrence was recorded in field books. Associated vegetation was recorded for each station.

We collected *C. maculata* soil samples from stations No. 3, 6, and 8 (Table 1) and compared them to two samples from habitats occupied by *C. mertensiana* on Douglas Island (58°18′N, 134°41′W), which is located in Stephens Passage near the south end of Lynn Canal. Each sample comprised multiple excavations made to rooting depth with a hand trowel. The samples were refrigerated after collection, and were analyzed by Waypoint Analytical (Richmond, VA) for percent organic matter; ppm P, K, Mg, and Ca; pH; and cation exchange capacity (CEC, meq/100 g). Each sample represented a replicate for statistical analysis. The data were square root-transformed and tested for differences between

TABLE 1. SOURCE, HABITAT CHARACTERISTICS, AND LOCATIONS FOR *CORALLORHIZA MACULATA* STATIONS IN ALASKA. Distances are linear map projections. Soil series are from McCloskey (1988) and Mulligan (2015). ALA = University of Alaska Herbarium; OS = Ohio State University Herbarium.

Station No.	Source material	Habitat	Location
1	Parker et al. 2000 No. 9993, ALA Cat. No. 34529; *C. maculata* var. *maculata.*	Steep rocky west slope; 60-450 m elev.; undescribed Cryorthents soil; *Picea sitchensis* forest.	11.3 km NW Haines; AK, Mt. Ripinski Trail; 59°16′N, 135°36′W.
2	Clineman-Ergle, 2007 *s.n.*, Acc. No. 00493, KLGO Cat. Nos. 50445-6; *C. maculata* var. *maculata.*	River floodplain; 17 m elev.; undescribed Cryorthents soil; open *Picea sitchensis* forest.	0.25 km E Dyea, AK; Taiya River, Skagway-Klondike Gold Rush National Historical Park; 59°30′14.7″N, 135°21′22.2″W.
3	Hall-Jacobson, Bowles, 2019 No. 19-1, OS; C. maculata var. *maculata.*	Steep rocky northwest slope, 100 m elev.; Krubate soil series; *Picea sitchensis-Tsuga heterophylla* forest.	9 km SE Haines, AK; Chilkat Peninsula; 59°9′50′′N, 135°23′31′′W.
4	Hall-Jacobson, 2020 No. 20-1, OS; *C. maculata* var. *maculata.*	Glacial alluvial fan, 10 m elev.; Nataga soil series; *Picea sitchensis-Alnus viridis* forest.	15 km S Haines, AK; Davidson Glacier; 59°5′20″N, 135°24′47″W.
5	Hall-Jacobson, 2020 No. 20-2, OS; *C. maculata* var. *maculata.*	Moderate rocky west slope; Krubate soil series, 60 m elev.; *Betula papyrifera - Tsuga heterophylla* forest.	12 km SE Haines, AK; Chilkat State Park; 59°7′57.954″N, 135°22′1.53″W.
6	Furbish, 2020 *s.n.*, OS; *C. maculata* var. *maculata.*	Low southeast slope, 150 m elev.; undescribed Haplocryod soil; *Betula papyrifera- Picea sitchensis* forest.	1.6 km NW Skagway, AK, Dyea Rd; 59°27′59″N, 135° 19′1″W.
7	Bowles, field observation 2019; *C. maculata.*	Steep west slope, 250 m elev.; undescribed Cryorthents soil; *Pinus contorta var. latifolia-Populus trichocarpa* forest.	24 km NW Haines, AK; Smith Cabin trail; 59°19′N, 135°43.6′W.
8	Bowles, Hall-Jacobson, field observation 2019; *C. maculata.*	River terrace, 30 m elev.; Lutak soil series; *Picea sitchensis-Populus trichocarpa* forest.	30.5 km NW Haines, AK; Chilkat River boat launch trail; 59°22′47″N, 135°50′22″W.

C. maculata and *C. mertensiana* samples using a t-test assuming unequal variances using NCSS 9 statistical software (NCSS, LLC. Kaysville, Utah, USA). Soil acidity was also measured for Station No. 4 using a portable pH meter and 1:1 soil: water solution. Though *C. mertensiana* occurs throughout Southeast Alaska, these samples provide a context for comparing soils from habitats near Lynn Canal and habitat for *C. maculata*.

Results

Climate

Growing season norms differed significantly among seasons and climate divisions (Fig. 1). Temperatures were intermediate for the Central Panhandle, about one degree C greater for the North Panhandle and lower for the Northeast Gulf. In contrast, precipitation was intermediate for the North Panhandle, about twice as great for the Central Panhandle and about one-third lower for Northeast Gulf. Although these patterns were similar for spring and summer, summer norms were significantly higher (Appendix 1). Within seasonal comparisons, North Panhandle summer temperatures also differed from summer temperatures in both the Central Panhandle and Northeast Gulf, while summer precipitation differed only from the Central Panhandle. For spring temperatures, the North Panhandle differed only from the Northeast Gulf. For spring precipitation, the North Panhandle differed from the Central Panhandle (Appendix 1).

Herbarium Studies

The ARCTOS data base contained 41 specimens of either *Corallorhiza maculata* or *C. mertensiana* (Appendix 2). One specimen (Parker et al. 2000 No. 9993, UAM Herb 34519) clearly represents *C. maculata* var. *maculata*, but had been identified as *C. maculata* subsp. *mertensiana*. This specimen was collected about 11 km northwest of Haines from a steep rocky west-facing slope at 60-450 m elevation under *Picea sitchensis* (Station 1, Table 1). This habitat appears to represent an undescribed Cryorthents soil with a thin organic matter layer developed over gravely silt or sandy loam residuum over metamorphic rock (McCloskey 1998). A second ARCTOS specimen (Batten and Juday 1988 No. 88-735, UAM Herb 26283) identified as *C. maculata* is in an advanced stage of fruit formation. This specimen may represent *C. maculata,* as it has reduced perianth size compared to fruiting *C. mertensiana* specimens. The collection site occurs on Anyaka Island, an extension of the Chilkat Peninsula, about 10 km south of a known *C. maculata* population (see below).

Fourteen ARCTOS *C. mertensiana* specimens were identified as *C. maculata* (six by the original collectors, and eight by annotations). The eight specimens annotated as *C. maculata* were subsequently annotated as *C. mertensiana*. Ten *C. mertensiana* specimens were identified as *C. maculata* subsp. *mertensiana* (four by the original collectors, and six by annotations). Three of these ten specimens were subsequently annotated as *C. mertensiana*. Another *C. mertensiana* specimen had been identified as *Monotropa hypopitys* L., but correctly annotated.

The remaining 14 *C. mertensiana* specimens were identified as such by the original collectors and were not annotated differently.

Among regional herbaria, the Klondike Goldrush National Historical Park herbarium contained two duplicate *C. maculata* var. *maculata* specimens with identical collection coordinates, dates and accession numbers, and sequential catalogue numbers (Station 2, Table 1). One specimen (Ergle-Clineman 2007 *s.n.*, KLGO Cat. No.50445) was identified as *C. maculata* and subsequently annotated as *C. mertensiana*. The second specimen (Clineman-Ergle, 2007 *s.n.* , KLGO Cat. No 50446) was identified as *C. mertensiana*. The collection site is in the Klondike Goldrush National Historical Park on the alluvial plane of the Taiya River, about 6 km northwest of Skagway, AK. The habitat represents an undescribed Cryorthents soil developed in gravelly alluvium (Mulligan 2015) supporting an open *Picea sitchensis* forest (Flagstad and Boucher 2015). The Glacier Bay NP herbarium contained two collections of *C. mertensiana* that were identified as *C. maculata* (Streveler 1969 *s.n.*, GB Cat. No. 753, Streveler 1970 *s.n.*, GB Cat. No 1515). The USFS Forestry Sciences Lab herbarium contained seven *C. mertensiana* specimens that were correctly identified. It also contained two duplicate *C. trifida* collections that had been identified as *C. maculata* (Flory, 1925 No. F-268, FSL Cat. No. 58609). The Alaska State Museum herbarium contained six specimens of *C. mertensiana* that were correctly identified. Review of orchid specimen images from the USFS herbarium, Yakutat revealed no *C. maculata* or *C. mertensiana* collections.

Field Studies

Our fieldwork identified six stations for *C. maculata*, all of which occur within the immediate drainage of upper Lynn Canal (Fig. 3). Four are represented by collections of var. *maculata* (Table 1), of which three occurred along the Chilkat River Inlet. A 2019 collection (Station 3, Table 1) occurred near sea level 9 km south of Haines on the east side of the Chilkat River Inlet. The habitat overlies glacial outwash supporting the Krubate soil series (McCloskey 1998). The plants occur on a west slope under *Picea sitchensis* and *Tsuga heterophylla* with occasional *Betula papyrifera* and *Pinus contorta* var. *latifolia*. The forest floor had a dense cover of the mosses *Hylocomium splendens* (Hedw.) B.S.G. and *Rhytidiodelphus loreus* (Hedw.) Warnst. Associated herbaceous plants include *Gymnocarpium dryopteris* (L.) Newman, *Orthilia secunda* (L.) House, the orchid *Goodyera oblongifolia* Raf., and *Pyrola chlorantha*

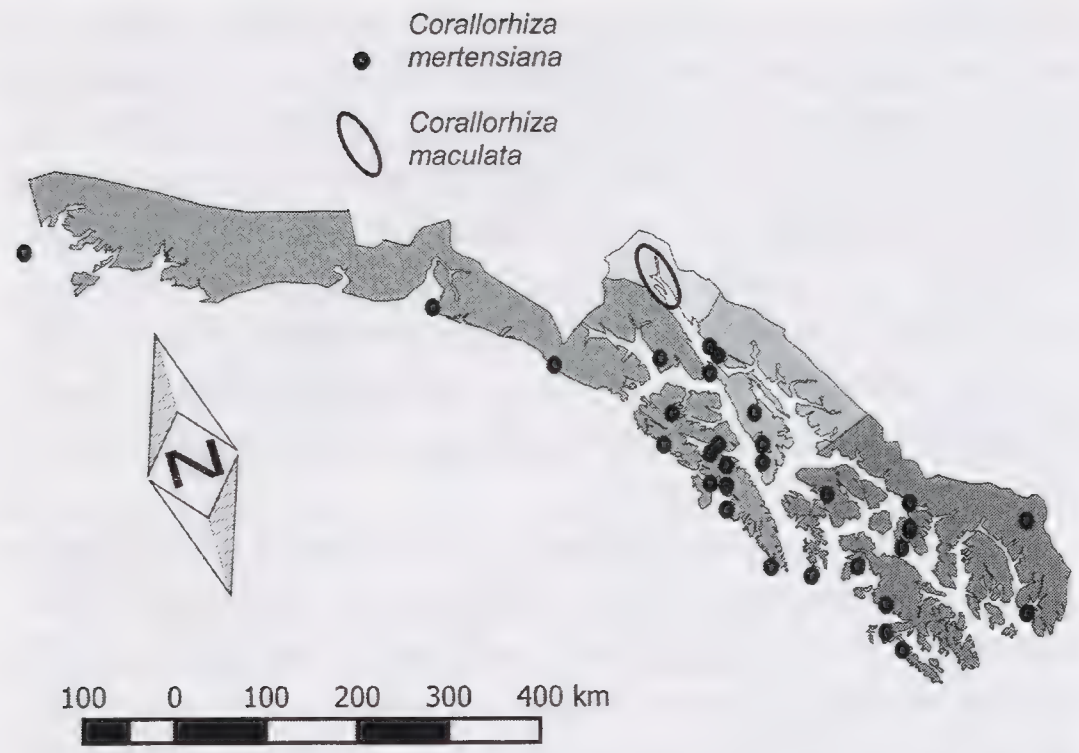

FIG. 3. Distribution of *Corallorhiza mertensiana* (solid dots representing Appendix 2) and *C. maculata* (ellipse including stations from Table 1) in Alaska. See Fig. 1 for climate divisions.

Sw. Two additional collections were made along the Chilkat River Inlet in 2020. One collection (Station 4, Table 1) occurred 15 km south of Haines on the alluvial fan of Davidson Glacier. This habitat supports the Natago soil series (McCoskey 1998); its dominant vegetation is *Picea sitchensis* forest with *Alnus viridis* (Chaix) DC. subsp. *sinuata* (Regel) A.Löve & D.Löve. The second collection (Station 5, Table 1) occurred 12 km southeast of Haines in the Chilkat State Park. The habitat is a rocky west slope over glacial outwash that also comprises the Krubate soil series (McCloskey 1998). It supports a *Betula papyrifera-Tsuga heterophylla* forest with *Gymnocarpium dryopteris*, *Goodyera oblongifolia*, *Oplopanax horridus* (J.E.Smith) Miq. and *Streptopus amplexifolius* (L.) DC. in the ground layer. A fourth collection (Station 6, Table 1) occurred 1.6 km northwest of Skagway, along Dyea Rd, and 5 km southeast of the KLGO specimen location. This habitat is a low southeast slope that appears to represent an undescribed Haplocryod soil developed in gravelly colluvium over residuum (Mulligan 2015). It supports a *Betula papyrifera-Picea sitchensis* forest. *Oplopanax horridus*, *Gymnocarpium dryopteris*, *Cornus canadensis* L. and *Pyrola asarifolia* Michx. occur in the understory.

We recorded *C. maculata* from two additional localities northwest of Haines (Table 1). One site (Station 7, Table 1) is located about 18 km northwest of Haines along the Haines highway, at 250 m elevation on a steep west slope forested with *Pinus contorta* var. *latifolia*, *Populus trichocarpa* and *Betula papyrifera* and the shrub *Shepherdia canadensis* (L.) Nutt. Associated herbaceous plants included the orchids *Calypso bulbosa* (L.) Oakes var. *americana* (R.Br.) Luer and *Goodyera oblongifolia*, as well as *Linnaea borealis* L., *Arctostaphylos uva-ursi* (L.) Spreng., *Arnica cordifolia* Hook. and *Chimaphila umbellata* (L.) W. P. C. Barton. This habitat also appears to represent an undescribed Cryorthents soil (McCloskey 1998). The second site (Station 8, Table 1) is located 27 km northwest of Haines along the Haines Hwy on a forested terrace of the Chilkat River, where plants occur under a canopy of *Picea sitchensis, Populus trichocarpa*, and *Shepherdia canadensis*. Associated herbs included the orchids *Cypripedium montanum* Douglas ex Lindl. and *Coeloglossum viride* (L.) Hartm.var. *virescens* (Muhl. ex Willd.) Luer, as well as *Pyrola asarifolia*. This habitat is developed in glacial fluvial sediments, with silt deposits overlying sand and gravel, and belongs to the Lutak soil series (McCloskey 1998). The plants noted at both stations were small-statured and occurred as single stems, which are characteristics of var. *maculata*.

In southern Lynn Canal, *C. mertensiana* usually occurs in sheltered near-coastal environments, often on slopes of uplifted sea bluffs (Motyka 2003) forested with *Picea sitchensis* and *Tsuga heterophylla*. A frequent associate is the orchid *Goodyera oblongifolia*. Soils for this habitat usually belong to the Tolstoi-McGilvery complex, which is characterized by <10 cm of well-drained forest litter developed over bedrock (Schoephorster and Furbush 1974).

Soil samples from habitats of both *C. maculata* and *C. mertensiana* were acidic and tended to be nutrient poor; but differed significantly ($P \leq 0.05$) for all variables except pH (Table 2). Samples for *C. maculata* represent the Lutak and Krubase soil series as well as an undescribed Haplocryod soil. They averaged <35% organic matter, about 16 ppm P, 100 ppm K, 127 ppm Mg, and 1290 ppm Ca, with about 11 meq/100 g CEC and 5.47 pH. Acidity of a Cryorthents soil sample from Station No. 7 was measured as pH = 5.9. These soils also have extremely low percent organic matter (McCloskey 1998). The *C. mertensiana* samples were from forested sea bluff habitat and appear to represent Tolstoi-McGilvery soils. These samples had over twice the content of organic matter (80%) as those from *C. maculata* habitats, but had an order of magnitude lower nutrient levels and CEC, and averaged 4.6 pH.

DISCUSSION

The *Corallorhiza maculata* Clade in Alaska

Our herbarium and field studies indicate that *Corallorhiza maculata* var. *maculata* has been established in Southeast Alaska since at least the year 2000. Although recent long-distance dispersal cannot be ruled out for orchids (e.g., Arditti and Ghani 2000), the occurrence of multiple stations in natural habitats suggests that they are a native component of the naturally occurring vegetation in this area. All known occurrences are within the climatically distinct North Panhandle Climate Division, which includes the upper reach of Lynn Canal (Fig. 3). The sister species *Corallorhiza mertensiana* is widespread in Southeast Alaska (Fig. 3), but does not occur in the North Panhandle Climate Division. It also occupies different habitats, tending to be associated

TABLE 2. AVERAGE AND STANDARD ERROR (SE) OF PERCENT ORGANIC MATTER (OM), CONCENTRATIONS OF P, K, MG AND CA (PPM), PH, AND CATION EXCHANGE CAPACITY (CEC) OF SOIL SAMPLES FROM *CORALLORHIZA MACULATA* AND *C. MERTENSIANA* HABITATS. Test statistics and probabilities represent the results of unequal variance t-tests. See text for sources of soils samples.

Species	Statistic	OM (%)	P	K	Mg	Ca	pH	CEC (meq/100 g)
C. maculata	Average	34.37	16.33	102.33	127.33	1290.00	5.47	10.73
	SE	10.25	4.90	15.92	16.74	513.58	0.78	1.22
C. mertensiana	Average	80.1	1	3	2	35.5	4.6	0.45
	SE	0.3	0	1	1	9.5	0.1	0.25
t		-4.9343	6.9435	13.2415	5.8448	4.0697	1.5029	8.0700
Prob		0.0386	0.0201	0.0013	0.0224	0.0530	0.2637	0.0040

with coastal rainforest and strongly organic soils. As a result, though both coralroot species occur in Southeast Alaska, their distributions are narrowly allopatric in this region.

Despite the absence of *C. maculata* from Alaska in both regional (Anderson 1959; Hultén 1968; Welsh 1974) and North American (Correll 1950; Magrath and Freudenstein 2002) treatments, 14 (25%) of the *C. mertensiana* specimens we examined had been identified or annotated as *C. maculata*. In contrast, three valid Alaskan specimens (two are apparently duplicates) of *C. maculata* had been identified as *C. mertensiana*. A fourth specimen in an advanced stage of fruit formation may have been correctly determined as *C. maculata*.

The sources of confusion that led to these determinations may have been related to the extreme rarity of true *C. maculata* material from Alaska and its absence from regional floras, as well as unfamiliarity of regional workers with this species' morphology and natural history. Workers following Calder and Taylor (1965), also might have identified specimens only to the species level. Calder and Taylor (1968) relegated *C. mertensiana* to a subspecies of *C. maculata,* contending that the material they examined had overlapping lip characteristics. Nevertheless, they acknowledged key characters separating these species, including differences in flower structure, and lengths of the column and mentum. Although *C. mertensiana* may have a solid-colored lip, most Alaskan specimens tend to have spotted or streaked lips (Hultén 1968). As suggested by Calder and Taylor (1968) this also may have led to confusion with *C. maculata*, which has a spotted lip as well.

Little specific information is available on habitat requirements of *C. maculata*, and they may vary across the wide range of this species. Calder and Taylor (1968) indicated that *C. maculata* (as *C. maculata* subsp. *maculata*) occurs in the dryland interior of northcentral and southeastern British Columbia, and dry woods on Vancouver Island. Although the known range of extant *C. maculata* populations in Alaska is quite restricted (Fig. 3), there does not appear to be an extremely narrow habitat niche for this species, as plants occur along an altitudinal gradient from near sea level to lower mountain slopes and occupy multiple soil types. This suggests that occurrences of these populations may be more dependent upon climate than soils or microhabitat. Nevertheless, the differences in soil characteristics between selected habitats for *C. mertensiana* and *C. maculata* may have bearing on the presence of *C. maculata* in Alaska if it requires greater soil fertility (e.g., Correll 1950). In addition, the lower percentage of organic matter in soils supporting *C. maculata* could interact with relatively low precipitation and high temperatures to further reduce soil water holding capacity of these forest habitats (e.g., Werner et al. 2020). As a result, available soil moisture in *C. maculata* habitats may be even lower than expected based on direct comparison of precipitation between climate divisions.

Because *Corallorhiza* are obligate mycoheterotrophs, the presence of their associated fungi must also play a part in determining distribution of the plant. Taylor and Bruns (1999) found that *C. maculata* and *C. mertensiana* both associate with *Russula* (Basidiomycota), but not with the same species, even when the plants are growing together in the same habitat.

A hypothesis explaining the distribution of *Corallorhiza maculata* in Alaska

Past plant migration in relation to deglaciation and climate change is an important driver of plant distribution in Alaska (e.g., Hultén 1968; Heusser 1960; Anderson 1995). The Alaska stations for *C. maculata* represent a 650 km range extension northwest of locations in central British Columbia. Multiple hypotheses can be advanced to explain this distribution. It may represent relics of a pre- or post-glacial distribution, or post-glacial migration through a suitable habitat corridor. Alternatively, this distribution may be an artifact of a gap in collection data. However, the more uniform distribution of *C. mertensiana* (Fig. 3) suggests that plant collection may have occurred across this distributional gap. We hypothesize that *C. maculata* migrated northward during the post-glacial Xerothermic (Hypsithermic) interval and now persists as relic populations in the rain shadow habitat of upper Lynn Canal. The Xerothermic warming event was maximized between 10-7500 BP in southwest British Columbia (Mathewes and Heusser 1981), and could

have facilitated northern migration through a drier intermountain corridor in west-central British Columbia (e.g., Alley 1976). The *C. maculata* specimen localities mapped by Szczawinski (1959) and Douglas et al. (2002) for northern British Columbia lend support to the hypothesis of a post-glacial migration northward through this region. The specific variety of these specimens is unknown. A 2006 photograph from the same general area is labeled as *C. maculata* v. *maculata* on the Electronic Atlas of the Flora of British Columbia (Klinkenberg 2018).

Other vascular plant and bryophyte distributions in Alaska also provide support for this hypothesis. For example, at least six other vascular plant species occur as northern disjuncts in Southeast Alaska as well as in western British Columbia and the adjacent Yukon Territory: *Lactuca biennis* (Moench) Fern, *Festuca occidentalis* Hook., *Agoseris glauca* (Pursh) Raf., *Sedum divergens* S.Watson, *Symphoricarpos albus* (L.) Blake, and *Chimaphila umbellata* (Hultén 1968; Murray 1980; Pavlick 1983; Parker 2001; Douglas et al. 2002). These species appear to have individualistic distributions and habitat requirements, and more work would be needed to determine the degree to which they have similar migration histories. Also, Worley (1972) suggested that upper Lynn Canal provides an immigration route for continental and oceanic bryophytes, and that relic populations persist from the Hypsithermic Interval in specialized habitats within that area.

In coastal British Columbia, Calder and Taylor (1968) contended that a northern migration of a flora adapted to dry southern habitat took place across the Haida Gwaii archipelago during the Xerothermic interval, leaving such species restricted to dry habitats. Strong and Hills (2003) also provided evidence that nine plant species, including the coralroot orchid *C. striata* Lindley, are disjunct in northern Alberta due to a northern migration during the Hypsithermic Interval, and were isolated in favorable habitat by post-hypsithermic cooling. They modeled a 1°C July temperature shift as a threshold for migration, which is similar to the temperature differences characterizing the North Panhandle Climate Division (Fig. 2). Likewise, Axelrod (1981) found a 1°C temperature shift responsible for migration of disjunct plant species in Central California during the Xerothermic Interval.

Our work on *C. maculata* accesses portions of two watersheds in a relatively small accessible portion of the upper Lynn Canal area. Botanical exploration for this species is needed in adjacent areas of the U.S. and Canada with similar climatic conditions as well as transboundary river drainages such as the upper Stikine River valley. Such information might expand knowledge of the distribution of *C. maculata,* how it migrated to this area, and whether it persists under specilaized climatic or habitat conditions, as well as the scale and type of such environments (e.g., Ashcroft 2010). Our data support the presence of *C. maculata* var. *maculata* in Alaska. Although we have no evidence of var. *occidentalis* in Alaska, this variety may co-occur with var. *maculata*, and is also present in central British Columbia (Freudenstein 1997). This variety should be sought as well. This information would also contribute to understanding how climate change during the Xerothermic Interval affected plant migration in the Pacific Northwest, and how such responses may help model effects of modern climate change on vegetation of this region (e.g., Peterson et al. 2014).

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APPENDIX 1. STATISTICAL COMPARISON OF MEAN (SE) TEMPERATURE (C) AND PRECIPITATION (MM) BY SEASON AMONG AND WITHIN CLIMATE DIVISIONS (BIENIEK ET AL. 2012). Tests are Kruskal-Wallis one-way ANOVA on ranks. Climate division means with identical lower case letters across rows are not significantly different with Kruskal-Wallis Multiple Comparison Z-Value Test ($\alpha = 0.05$). See Figure 1 for climate division locations and growing season comparisons.

			Climate division							
			Central panhandle		North panhandle		Northeast Gulf		Kruskal-Wallis	
	Measure		Mean	SE	Mean	SE	Mean	SE	X^2	Prob
Spring	Temperature		11.02[a]	0.32	11.75[a]	0.32	9.88[b]	0.20	23.54	< 0.001
	Precipitation		9.06[a]	0.68	4.57[b]	0.55	3.13[b]	0.20	49.96	< 0.001
Summer	Temperature		13.66[a]	0.18	14.20[b]	0.17	13.27[a]	0.13	16.04	< 0.001
	Precipitation		14.98[a]	0.99	6.54[b]	0.73	5.13[b]	0.30	64.78	< 0.001
Kruskal-Wallis	Temperature	χ^2	32.517		30.786		97.381			
		Prob	<0.001		<0.001		<0.001			
Kruskal-Wallis	Precipitation	χ^2	17.122		4.142		25.090			
		Prob	<0.001		0.042		<0.001			

APPENDIX 2. *CORALLORHIZA MACULATA* AND *CORALLORHIZA MERTENSIANA* SPECIMENS ACCESSED ON ARCTOS.

Catalog no.	Collector; original identity	Collection date; no.	Locality	Annotations	Species identity
UAM Herb 26283	A.R.Batten, J.P.Juday; *C. maculata*	1988/09/02; No. 88-735	Lynn Canal, Anyaka Is., T32S,R60E,S34		*C. maculata?*
UAM Herb 34519	C.L.Parker et al.; *C. maculata* subsp. *mertensiana*	2000/07/23; No. 9993	St. Elias Mts., Mt. Ripinski trail, Mile 7 Haines Hwy., lower portion of trail		*C. maculata* var. *maculata*
UAM Herb 26281	J.Ver Hoef; *C. maculata*	1982/06/30; No. 585	Etolin Is., Steamer Bay		*C. mertensiana*
UAM Herb 26282	S.Lewis, K.Max; *C. maculata*	1988/06/24; No. 85	Coronation Is.		*C. mertensiana*
UAM Herb 10602	S.Lewis; *C. maculata*	1993/07/08; No. *s.n.*	Dall Island, Foul Bay		*C. mertensiana*
UAM Herb 11609	C.L.Parker; *C. maculata*	1994/06/26; No. 5101	Craig, Prince of Wales Is.		*C. mertensiana*
UAM Herb 11087	C.L.Parker; *C. maculata*	1994/07/19; No. 5362	Kadin Is., mouth of Stikine River, S end of island		*C. mertensiana*
UAM Herb 43744	S.H.Warner; *C. maculata*	1982/08/08; No. 13	Northern Admiralty Is.	L. Magrath (1989-90 FNA), *C. mertensiana*	*C. mertensiana*
UAM Herb 41553	J.P.Anderson; *C. mertensiana*	1939/07/01; No. 5584	Coast Mts., Hyder	J.R. Grant (1989 ALA), *C. maculata*; L. Magrath (1989-90 FNA), *C. mertensiana*	*C. mertensiana*
UAM Herb 50930	R.Thomas; *C. mertensiana*	1952; No. 60	Yakutat Foreland, Yakutat	J.R. Grant (1989 ALA), *C. maculata*; L. Magrath (1989-90 FNA), *C. mertensiana*	*C. mertensiana*
UAM Herb 42313	R.Brown; *C. mertensiana*	1966/07/00; No. *s.n.*	Kupreanof Is.	J.R. Grant (1989 ALA), *C. maculata*; L. Magrath (1989-90 FNA), *C. mertensiana*	*C. mertensiana*
UAM Herb 42922	W.Robuck; *C. mertensiana*	1967/06/19; No. 97	Lindenberg Head, Chichagof Is.	J.R. Grant (1989 ALA), *C. maculata*; L. Magrath (1989-90 FNA), *C. mertensiana*	*C. mertensiana*
UAM Herb 42921	M.C.Muller; *C. mertensiana*	1980/06/17; No. 3522	Hanus Bay, Baranof Is.	J.R. Grant (1989 ALA), *C. maculata*; L. Magrath (1989-90 FNA), *C. mertensiana*	*C. mertensiana*
UAM Herb 42920	M.C.Muller; *C. mertensiana*	1981/08/02; No. 4538	Eliza Harbor, Admiralty Is.	J.R. Grant (1989 ALA), *C. maculata*; L. Magrath (1989-90 FNA), *C. mertensiana*	*C. mertensiana*
UAM Herb 42141	A.Johnstone, M.K.Muller; *C. mertensiana*	1982/07/04; No. 5168	Picnic Cove, 12 mi. S of Sitka, Baranof Is.	J.R. Grant (1989 ALA), *C. maculata*; L. Magrath (1989-90 FNA), *C. mertensiana*	*C. mertensiana*
UAM Herb 43743	M.C.Muller; *C. mertensiana*	1982/07/19; No. 5173	Eight Fathom Bight, Port Frederick, Chichagof Is.	J.R. Grant (1989 ALA), *C. maculata*; L. Magrath (1989-90 FNA), *C. mertensiana*	*C. mertensiana*
UAM Herb 9948	J.DeLaup, M.Duffy; *C. maculata* subsp. *mertensiana*	1993/07/07; No. 93-296	Foggy Bay, Eagle Nest Is.		*C. mertensiana*
UAM Herb 123885	W.Robuck; *C. maculata* subsp. *mertensiana*	1972/; No. 1350	Hyder, steep slope above U.S. custom house		*C. mertensiana*
UAM Herb 41747	B.J.Neiland; *C. mertensiana*	1960/07/31; No. 102	Coronation Is., Egg Harbor	AR.Batten (1990 ALA), *C. maculata* subsp. *mertensiana*	*C. mertensiana*
UAM Herb 42919	B.J.Neiland; *C. mertensiana*	1964/06/26; No. 1071	Baranof Is., Sitka, Totem Trail	AR.Batten (1990 ALA), *C. maculata* subsp. *mertensiana*	*C. mertensiana*
UAM Herb 41745	B.J.Neiland; *C. mertensiana*	1964/07/08; No. 1193	Coronation Is., Egg Harbor	AR.Batten (1990 ALA), *C. maculata* subsp. *mertensiana*	*C. mertensiana*
UAM Herb 41746	B.J.Neiland; *C. mertensiana*	1964/08/15; No. 1277	Craig, Prince of Wales Is., ca. 5 mi. Kluwak Road	AR.Batten (1990 ALA), *C. maculata* subsp. *mertensiana*	*C. mertensiana*
UAM Herb 42314	D.Klein (no ID)	1959/07/09; No. 511	Drag Is., between Etolin and Woronkofski Is.	P.Rutledge (1969), *C. maculata* subsp. *mertensiana*	*C. mertensiana*

APPENDIX 2. CONTINUED

Catalog no.	Collector; original identity	Collection date; no.	Locality	Annotations	Species identity
UAM Herb 42923	L. Smith; *C. maculata* subsp. *mertensiana*	1958/06/23; *s.n.*	Baranof Is., 4 mi E. Sitka, between Hart and Thimbleberry lakes	L. Magrath (1989-90 FNA), *C. mertensiana*	*C. mertensiana*
UAM Herb 41748	L.Vorobik, J.Solberg; *C. maculata* subsp. *mertensiana*	1979/06/27; No. 14	Prince of Wales Is., Sarkar Cove, E. of Deweyville	L. Magrath (1989-90 FNA), *C. mertensiana*	*C. mertensiana*
UAM Herb 42315	D.Klein (no ID)	1959/08/07; No. 479	Woronkofski Is., Sunset Peak	P.Rutledge (1989), *C. maculata* subsp. *mertensiana*, L.Magrath, *C. mertensiana* f. *alba*	*C. mertensiana*
UAM Herb 26284	K.Oakley; *C. mertensiana*	1978; No. 1978	Prince William Sound, Naked Is.		*C. mertensiana*
UAM Herb 10490	M.C.Muller; *C. mertensiana*	1992/06/30; No. 5674	Pack Cr. mouth, W side Seymour Canal, Admiralty Is.		*C. mertensiana*
UAM Herb 16740	H.Ulrich, MC.Stensvold; *C. mertensiana*	1993/09/01; No. 6325	Baranof Is., betw. south and middle arms of Kelp Bay, 300 ft E of log dump.		*C. mertensiana?*
UAM Herb 129408	B. Krieckhaus; *C. mertensiana*	2005/26/6; No. 402	Chichagof Is., back of Ford Arm		*C. mertensiana*
UAM Herb 192334	WJ. Weyerdam; *C. mertensiana*	1947/8/5; No. 5381	Wash. Bay	L. Magrath (1989-90 FNA), *C. mertensiana*	*C. mertensiana*
UAM Herb 192336	(V.F.?) Williams; *C. mertensiana*	1937; *s.n.*	Pleasant Hrbr	L. Magrath (1989-90 FNA), *C. mertensiana*	*C. mertensiana*
UAM Herb 192391	J.P.Anderson; *C. mertensiana*	1925/8/11; No. 2A297	Boat Hrbr. (Lynn Canal)	L. Magrath (1989-90 FNA), *C. mertensiana*	*C. mertensiana*
UAM Herb 192392	V.F.Williams; *C. mertensiana*	1940/7; *s.n.*	Baranof Is.	L. Magrath (1989-90 FNA), *C. mertensiana*	*C. mertensiana*
UAM Herb 192393	S.L.Welsh, G. Moore; *C. mertensiana*	1966/8/2; No. 6140	Auke Bay. 15 mi. N. Juneau	L. Magrath (1989-90 FNA), *C. mertensiana*	*C. mertensiana*
UAM Herb 192394	J.P.Anderson; *C. mertensiana*	1936/7/31; No. 2988	Craig	L. Magrath (1989-90 FNA), *C. mertensiana*	*C. mertensiana*
UAM Herb 192395	J.P.Anderson; *C. mertensiana*	1939/7/1; No. 5584	Hyder	L. Magrath (1989-90 FNA), *C. mertensiana*	*C. mertensiana*
UAM Herb 192396	J.P.Anderson; *C. mertensiana*	1927/8/4; No. 2A665	Ketchikan. Deer Mt.	L. Magrath (1989-90 FNA), *C. mertensiana*	*C. mertensiana*
UAM Herb 192726	I.L.Norberg; *C. mertensiana*	1932/8/3; No. 260	Chichagof Is., Hoonah	L. Magrath (1989-90 FNA), *C. mertensiana*	*C. mertensiana*
UAM Herb 240307	J.P.Anderson; *C. mertensiana*	1947/14; No. 37	Sitka	L. Magrath (1989-90 FNA), *C. mertensiana*	*C. mertensiana*
UAM Herb 42750	D.Weixelman; *Monotropa hipopitys*	1984/08/15; *s.n.*	Admiralty Is., Gambier Bay E of Snug Cove	AR. Batten (2002 ALA), *C. mertensiana*	*C. mertensiana*

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SMOKE-INDUCED GERMINATION IN THE ENDANGERED *ERIODICTYON CAPITATUM* (NAMACEAE)

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ABSTRACT

Understanding the germination cues of rare plants is critical to their conservation, restoration, and management. We used a greenhouse study to investigate the germination of *Eriodictyon capitatum* Eastw. (Lompoc yerba santa) seeds to understand the species' life history and to inform restoration efforts. *Eriodictyon capitatum* is a woody shrub that is listed as rare by the state of California and endangered by the U.S. Fish and Wildlife Service. Limited to just seven extant occurrences, *E. capitatum* does not currently readily produce seeds at most sites, but it does spread clonally, sometimes leading to low genetic diversity in aboveground vegetation. We collected seeds from one wild occurrence and measured germination rates in response to each of five physical treatments: control, dry heat, hot soak, liquid smoke, and scarification. Each physical treatment was replicated under both light and dark conditions. The highest percent germination was recorded with the liquid smoke treatment and the fastest germination occurred when seeds were sown in the dark and treated with liquid smoke. The significant impact of liquid smoke on seed germination suggests that *E. capitatum* is adapted to fire and that periodic fires could potentially promote aboveground genetic diversity by eliciting a flush of germination from the soil seed bank. These results can facilitate future propagation efforts, inform management, and also highlight the important role of fire in the life history of this endangered plant.

Key Words: Conservation, Eriodictyon, fire, germination, rare plant, smoke-induced, yerba santa.

The successful conservation and recovery of rare plant taxa is contingent upon an understanding of the biotic and abiotic conditions affecting their survival and reproduction, as well as the ecological networks to which they belong. Achieving this understanding requires studies of the biology, ecology, genetics, and horticulture of individual taxa, as well as the dynamics of populations, communities and ecosystems. However, many rare plant taxa and habitats remain understudied, likely due to a lack of funding and logistical challenges (Owen and Rosentreter 1992; Hessl and Spackman 1995). Although understanding germination behavior is critical to the successful conservation of seed-producing plants, information about this portion of the life cycle is often deficient (CPC 2019).

Understanding the germination requirements of rare plants not only facilitates propagation for activities that enhance conservation (e.g., conservation seed banks and living collections) and restoration, but can also provide insight into how natural processes, such as fire, influence the dynamics of rare plant populations within natural communities. Fire-adapted vegetation communities, including chaparral and sage scrub, have evolved with natural fire regimes and are composed of species that not only tolerate, but often require fire in order to complete their life cycles (Sugihara and Barbour 2006; Keeley et al. 2011b). Plant species inhabiting fire-prone environments often exhibit adaptive life history traits, including resprouting lignotubers, serotiny, and heat- or smoke-induced seed germination (Keeley 1987; Buhk et al. 2007; Keeley et al. 2011b). Diverse germination patterns have been observed in chaparral vegetation, where some seeds are described as "refractory," requiring fire-related cues for germination, or non-refractory, describing a syndrome under which plants persist and proliferate during periods between fires (Keeley 1991). A similar evolutionary trajectory has also been observed in the South African fynbos, another fire-prone ecosystem (Keeley and Bond 1997). Some estimates suggest that as much as 54% of California's vegetation (by area) requires some level of exposure to fire to persist, illuminating the important ecological role of fire in maintaining California's diverse ecosystems (Barbour and Major 1988).

Previous work has shown significant increases in seed germination rates of common species, including *Eriodictyon crassifolium,* when exposed to smoke (Keeley 2005). Furthermore, fire disturbance creates favorable conditions for postfire obligate seeding, and certain species of *Arctostaphylos* have long-lived seed banks (Kelly and Parker 1990) cued by fire, which benefit from newly opened areas with reduced competition (Keeley et al. 2016). The conservation of at-risk, fire-adapted plant species, as well as their common native associates, depends not only on an

accurate understanding of the specific natural fire regime in which they evolved, but also on a detailed understanding of the role that fire plays in their biology. Despite general interest in fire-adapted germination cues, investigations into the effects of fire on germination in rare plants are notably sparse. Consequently, relatively little is known regarding the effects of fire on the life history of many rare plant taxa (Hessl and Spackman 1995; CNPS 2019).

The dynamic and sometimes controversial nature of fire in the modern era further complicates matters. For example, the 2017-2018 wildfire season resulted in the greatest loss of human life and property in California state history (CalFire 2019). The western U.S. as a whole has seen a steady increase in the number and intensity of wildfires over the past six decades, with 61% of all recorded fires from 1950-2017 having occurred since the year 2000 (Davis and Weber 2018). A growing body of research suggests that observed changes in climate may have already influenced wildfire potential globally (Gillett et al. 2004; Westerling et al. 2006; Flannigan et al. 2009), and predictive models forecast significant alteration of global wildfire regimes (Scholze et al. 2006; Flannigan et al. 2009; Moritz et al. 2012). In parts of California, an escalation in fire severity is expected within the next century (Brown et al. 2004; Barbero et al. 2015). Correspondingly, with an ever increasing need to protect human life and property, required fire suppression efforts may have previously and will continue to affect rare plant populations adapted to specific historic fire return intervals on both broad and localized scales. The overall inability to speak to the historic fire return interval at the population level, the absence of information on how fire may relate to rare flora's life history, and the increasing difficulty to control fire are confounding factors that complicate land management decisions.

The goal of this study was to understand the germination requirements of the endangered *Eriodictyon capitatum* Eastw. (Lompoc yerba santa) to inform conservation and restoration efforts. This knowledge will be essential in helping this species achieve recovery in the wild, particularly in the context of current and anticipated future alterations to historic fire regimes. Previous research indicates that *E. capitatum* is self-incompatible (Elam 1994), and that low genetic diversity within sites resulting from clonal reproduction may be an impediment to seed production (Elam 1994; USFWS 2011). Two of the known populations were previously identified as being uniclonal, with reported seed production ranging from extremely low to none (Elam 1994; H. Schneider personal observation). The inability to produce viable seed, and thus to establish and maintain a soil seed bank, could make uniclonal or low-diversity populations susceptible to environmental stochasticity.

No previous work has investigated seed germination cues in *E. capitatum*, and understanding the germination requirements of this species will aid in the recovery of uniclonal populations by creating a viable large-scale propagation pathway that is more efficient and effective than vegetative cuttings. Propagation from seed can be used to not only increase the number of plants in conservation collections and natural populations, but also to increase genetic diversity within existing stands. The ability to supplement uniclonal stands with novel genotypes could help land managers restore genetic diversity at the population-level to facilitate sexual reproduction, which would not be achievable without intervention.

Understanding the relationship between fire and *E. capitatum* recruitment will empower land managers to make informed decisions regarding habitat and fire management, including the potential application of prescribed burning as a restoration technique. Given that *E. capitatum* has the ability to quickly resprout following fire (Jacks et al. 1984), and that the species is known to occur in and near areas that have historically experienced regular fire (Mensing et al. 1999), we hypothesized that *E. capitatum* seeds might respond positively to fire-related germination cues.

METHODS

Study Species

Eriodictyon capitatum, commonly known as Lompoc yerba santa, is a woody evergreen shrub in the family Namaceae. The species was listed as rare by the California Department of Fish and Wildlife in 1979 and as endangered by the U.S. Fish and Wildlife Service in 2000 (USFWS 2000). *Eriodictyon capitatum* leaves are narrow and leathery with a distinctly resinous scent. Corollas are lavender in color and tubular in shape, with many flowers clustered in a capitate inflorescence at the tips of stem branches (Fig. 1). *Eriodictyon capitatum* is extremely limited in its geographic distribution, occurring only in a small portion of western Santa Barbara County, California, United States of America (USA), and is historically known from just eight locations within that region (CDFW 2020; Santa Barbara Botanic Garden [SBBG] unpublished data). Mean annual temperature for the area encompassing these occurrences is 14.9°C and mean annual precipitation averages 507 mm. Four occurrences are found on Vandenberg Air Force Base, three are on private property (two on Orcutt Hill oil fields, and one on Hollister Ranch, a private ranch community), and one occurrence is located within the Dangermond Preserve, which is owned by The Nature Conservancy (CDFW 2020; SBBG unpublished data). One occurrence on Vandenberg Air Force Base was recently discovered by contractors and mapped by the Santa Barbara Botanic Garden in 2019 (SBBG unpublished data); another has not been relocated since 1987, despite multiple survey efforts, and is presumed extirpated. The rest of the occurrences are either known or presumed extant.

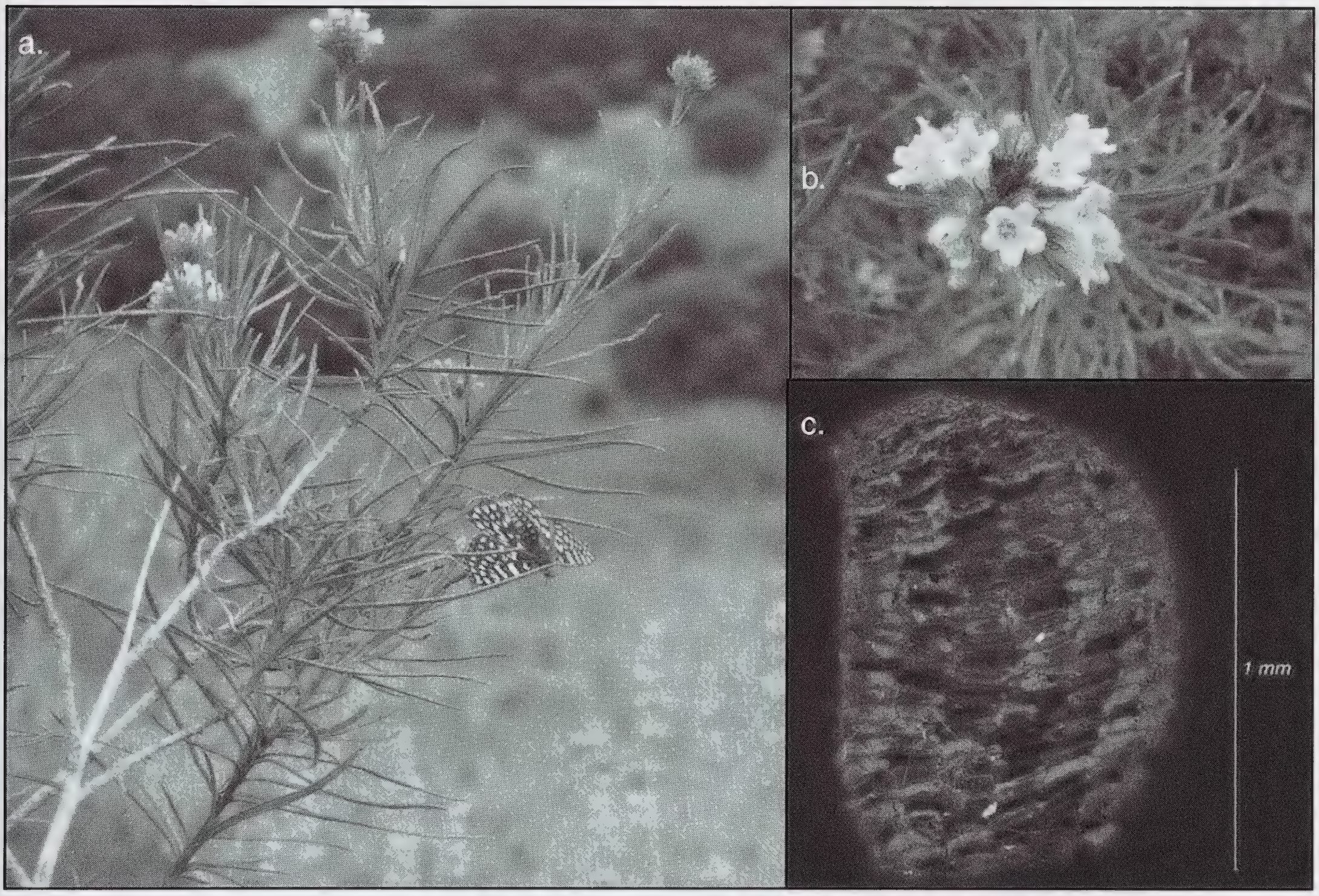

FIG. 1. *Eriodictyon capitatum* vegetation, flowers and seeds. A. leaves B. capitate inflorescence C. seed.

Like many of its congeners, *E. capitatum* is considered an early successional or "pioneer" species, exhibiting opportunistic resprouting in response to soil disturbance. When first describing the species, Wells (1962) observed that *E. capitatum* readily colonized roadsides and other disturbed areas. In addition, Jacks et al. (1984) observed that *E. capitatum* readily resprouted following fire at Vandenberg Air Force Base, although no seedlings were detected.

The ability to reproduce clonally via underground rhizomes facilitates colonization of disturbed areas, but *E. capitatum* also reproduces sexually via seed production, which is important for maintaining genetic diversity within populations. *Eriodictyon capitatum* plants are self-incompatible (Elam 1994) and require sufficient genetic variation within populations to produce viable seed via outcrossing. Although the pollinators of *E. capitatum* are unknown, other *Eriodictyon* taxa are known to be pollinated by wasps, bees, and butterflies (Moldenke 1976). Sweep netting of floral visitors to *E. capitatum* at Vandenberg Air Force Base yielded collections of *Bombus vosnesenskii*, *Lasioglossum incompletum*, and as-yet unidentified members of the Bombyliidae, Chrysomelidae, Formicidae, Melyridae families (Knapp unpublished data 2015). Previous work investigating floral visitors to an endangered congener, *E. altissimum*, identified ants, beetles, bumblebees, flies, and butterflies on and inside the corollas (Kofron et al. 2019b).

A population genetics study that included six of the known *E. capitatum* occurrences identified four as multiclonal and two as uniclonal (Elam 1994). Elam (1994) observed that uniclonal populations produced an average of <2 seeds per inflorescence. In addition to genetic constraints and self-incompatibility, Elam (1994) also identified other factors that could potentially affect seed production, such as the spatial distribution of clones, fruit parasitism, floral abundance and pollen quality. Recent surveys at a subset of occurrences have found that little to no viable seed is produced at multiple *E. capitatum* occurrences on Vandenberg Air Force Base and Hollister Ranch (H. Schneider, personal observation) and one uniclonal site on Vandenberg Air Force Base was observed to resprout after fire, but no seedlings were located (Jacks et al. 1984). To our knowledge, Orcutt Hill is the only location where *E. capitatum* reliably produces viable seed, likely due to the large number of plants at the site and presumed genetic diversity among plants. At the time of writing, we knew of no previous effort to investigate the germination requirements of *E. capitatum* seeds.

Field and Greenhouse Methods

Prior to germination testing, *E. capitatum* seeds were collected from wild plants in three zones (A, B, C; Fig. 2) at the Orcutt Hill oil fields in September 2018. Zones were determined based on the geography

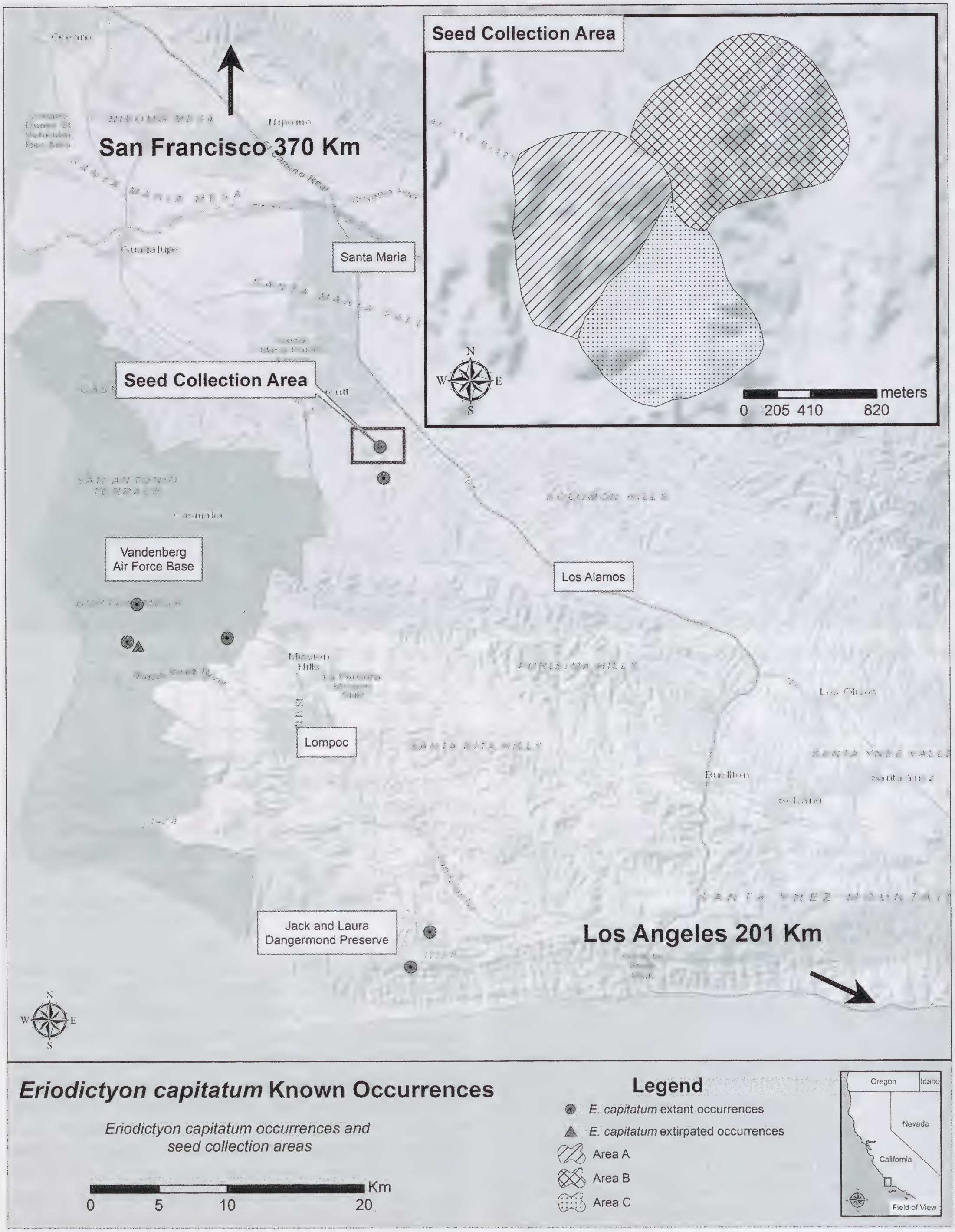

FIG. 2. Map of *Eriodictyon capitatum* geographic distribution and study site.

of the site and what appeared to be natural groupings of plants. Inflorescences were collected by hand into paper bags and transported to SBBG. Following collection, the seeds were treated with No Pest® Strip$_2$ (www.hotshot.com) to eliminate potential arthropod pests. Seeds were then cleaned in the lab and passed through an Advantech U.S.A. #25 Standard Testing Sieve to standardize seed size.

Smaller than average seeds and any seeds that showed evidence of predation or damage were excluded from this study.

Our experimental design was informed by a previous study that included *E. crassifolium* and suggested that the seeds are fire-adapted (Keeley 2005). Our methods were also informed by the observation that *E. capitatum* abundance oscillates in conjunction with disturbance events. Since *E. capitatum* is a disturbance-follower and appears to utilize gaps in chaparral vegetation, we hypothesized that *E. capitatum* seeds may survive for extended periods in the soil waiting for an appropriate germination cue. We tested the effects of five physical treatments on seed germination:

1. Control: No physical treatments were implemented.
2. Dry heat treatment: Seeds were heated in an oven at 100°C for 5 min.
3. Liquid smoke: Seeds were soaked in a 1:100 dilution of liquid smoke (Living Nutritionals all-natural pure liquid smoke, Livingnutritionals.com, Seattle, WA) and deionized water overnight.
4. Scarification: Seeds were placed into a seed de-awner and lightly rubbed with P120 (moderate grit) sand paper.
5. Hot soak: Seeds were placed into beakers and boiling (100°C) distilled water was poured over the seeds, which was then allowed to return to ambient temperature as the seeds soaked overnight.

*Each physical treatment was replicated under both light and dark conditions, as described below.

We were specifically interested in investigating the effects of two components of fire on *E. capitatum* germination: heat and smoke. To tease these two factors apart, we implemented both a dry heat treatment and a liquid smoke treatment, which are common germination treatments for fire-adapted species. We did not test the combination of these two factors. In the scarification treatment, we used sandpaper to mimic the effects of seeds existing in the soil seed bank for many years, which may cause physical abrasions to the seed coat. The hot soak treatment was designed to break the seed coat and facilitate imbibition.

In addition to the physical treatments, we also assessed germination under two different light conditions (i.e., light and dark) to determine whether seed burial or exposure to deep shade could affect germination rates. All physical treatments were administered under indoor light conditions and seeds were only subjected to darkness after they were plated in Petri dishes. In total, this study included 10 treatments with six replicates of 20 seeds each for a total of 120 seeds per treatment and 1,200 seeds overall. Each seed collection zone (A, B, C) was equally represented across all treatment combinations.

Seeds were germinated in Petri dishes on Difco™ Agar Bacteriological, a growing medium composed of polysaccharide agarose and agaropectin. The Petri dishes were placed in a Streamline® Polymerase Chain Reaction (PCR) Cabinet with a UV light for 24 hr to reduce the potential for contamination. Prior to implementing physical treatments, the *E. capitatum* seeds were treated with a 10% bleach solution for 1 min and all tools were sterilized to reduce mold or bacterial contamination in the dishes.

The liquid smoke and hot soak treatments were initiated on 4 February 2019, while the remaining physical treatments were implemented on 5 February 2019. Within 24 hr of physical treatment implementation, 20 seeds from the same treatment were plated in each Petri dish, which was numbered corresponding to the treatment and collection zone. Seeds were plated in the PCR cabinet with the vent on to reduce the risk of contamination. On 5 February 2019, Petri dishes subjected to the light treatment were placed in a screen house and exposed to ambient light. On the same day, dark treatment replicates were placed in the same screen house but were wrapped in multiple sheets of aluminum foil to prevent exposure to sunlight. SBBG is located approximately 56 miles southeast of the seed collection site and the climate in Santa Barbara is similar to the natural environments in which *E. capitatum* occurs. During the course of this study (February-June 2019), the dishes from all treatments were shielded from rain, but otherwise subject to ambient conditions, with mean daily temperatures ranging from 10.3°C in February to 16.7°C in June (MesoWest, 2019).

Petri dishes were monitored 3 d per week and germination, defined as visible radicle emergence, was recorded. Dark treatments were scored in a pitch-dark room under red LED light. Red light has been shown to promote germination in some species (as first described in lettuce by Borthwick et al. 1954), but exposure was brief, as dark treatment dishes were unwrapped and scored individually in approximately 1–2 min per dish. The dark treatment dishes also dehydrated more slowly than light treatment dishes, as being wrapped in foil decreased evaporation from the agar gel. Following germination, seeds were transplanted into soil in the greenhouse and surviving seedlings resulting from this study were transplanted into pots for inclusion in the garden's living collection and/or use in future research or restoration. Germination scoring ceased on 24 June 2019, 2 wk after the last germination event was recorded.

Following germination scoring, a subsample of Petri dishes was selected to receive cut tests to assess the potential viability of the remaining seeds. Potential viability was defined as the number of seeds that germinated divided by the number of seeds that appear viable following visual examination (e.g., a cut test) and is expressed as a percentage. Two Petri dishes from each treatment were chosen using a random number generator and all remaining seeds within those dishes were cut with a razor blade and examined under a microscope. Cut seeds were scored as either filled (i.e., potentially viable), empty, moldy (mold growing inside of the seed) or infested. Seeds that were empty (including partially filled), moldy or infested were recorded as inviable.

Despite multiple efforts to sterilize Petri dishes and seeds, mold growth was observed in several of the Petri dishes early in the experiment. In some cases, the mold was exclusive to agar and in others, mold was observed growing on seeds. When possible, moldy agar was excised from the dishes without disturbing seeds. In the first weeks of the study, some moldy seeds were also removed from the Petri dishes. Moldy seeds were saved to determine whether they were still viable. After observing that seeds with mold growing on the seed coat could germinate, we ceased removal of moldy seeds from the dishes. Mold growth slowed over the duration of the study and most seeds were not impacted by mold. Seeds that were internally moldy, as observed during a cut test, were deemed inviable. Three dishes from the control/dark and one dish from the scarification/dark treatment were removed from the study following an equipment malfunction that compromised seeds, reducing sample size for some treatments, resulting in a total of 960 seeds for analysis.

Data analysis

We analyzed germination rates based on the number of seeds remaining in each Petri dish after accounting for the early removal of moldy seeds and compromised dishes (i.e., the total number of seeds was <20 for some dishes). We analyzed germination data from 56 Petri dishes containing 960 seeds in the final analysis. A Kruskal-Wallis test used to evaluate the potential effect of the collection zone on germination rates detected no differences (data not shown), so all collection zones were analyzed together. The hot soak treatment resulted in zero germinated seeds, so those data were excluded from statistical analyses. For all analyses, significant differences were determined using $\alpha = 0.05$. All data were analyzed using JMP 13.0.0.

Observed germination rates. Observed germination rates were calculated as percentages within each Petri dish. The germination data were nonparametric and resisted transformation. Thus, we analyzed the data using Kruskal-Wallis tests followed by Wilcoxon pairwise comparisons to detect differences in germination rates between treatments. Physical and light treatments were analyzed together as a combined treatment (e.g., control/light).

Germination rates based on cut tests. In addition to observed germination rates, we also analyzed the germination rate of potentially viable seeds using the results of the cut tests on a subsample of seeds across 20 dishes. We calculated potential viability using the formula:

$$\%\ \text{germination of potentially viable seeds} = \frac{\#\ germinatedseeds}{(\#\ germinated + \#\ filledseeds)} \times 100$$

The cut test data were normally distributed and differences between treatments were analyzed using a full factorial analysis of variance (ANOVA) followed by a Tukey's HSD test to adjust for multiple comparisons.

TABLE 1. MEAN GERMINATION RATES BY TREATMENT. *n* represents the number of Petri dishes per treatment.

Treatments	*n*	Mean germination rate (%)	SD
Control/light	6	23.2	9.0
Control/dark	3	13.3	23.1
Dry heat/light	6	30.3	11.6
Dry heat/dark	6	35.3	17.3
Hot soak/light	6	0	0
Hot soak/dark	6	0	0
Liquid smoke/light	6	74.6	10.0
Liquid smoke/dark	6	92.4	5.5
Scarification/light	6	24.0	12.6
Scarification/dark	5	20.5	12.6

Days to first germination. We calculated the number of days between sowing seeds and the first germination observation to determine whether seeds in some treatments germinated more quickly than others. We investigated the "speed" of germination in two ways: first, by comparing treatments to each other and second, by comparing light and dark treatments within each physical treatment. The data were nonparametrically distributed. Kruskal-Wallis tests were used to analyze treatment effects and Wilcoxon pairwise comparisons were used to assess differences between treatments when appropriate.

RESULTS AND DISCUSSION

Observed Germination Rates

Germination rates across treatments ranged from 0-92.4% (Table 1). Zero seeds germinated in the hot soak treatment, regardless of light treatment, so those data were excluded from further statistical analyses.

The liquid smoke treatment elicited the strongest germination response, with dark conditions appearing to confer an added benefit that resulted in germination rates greater than 90%. The second most effective treatment was dry heat, with a mean of 30-35% germination, depending on whether or not seeds were exposed to light. There was no statistical difference in germination rates between the other treatments, regardless of whether seeds were germinated under light or dark conditions (Fig. 3).

Germination Rates Based on Cut Tests

We cut seeds from a subsample of dishes (n=20 dishes). Of 222 seeds cut, 183 appeared viable, 11 were empty or partially filled and 28 seeds were found to be internally moldy. None of the seeds we cut showed signs of infestation by insects or other granivores. Filled seeds appeared healthy under the

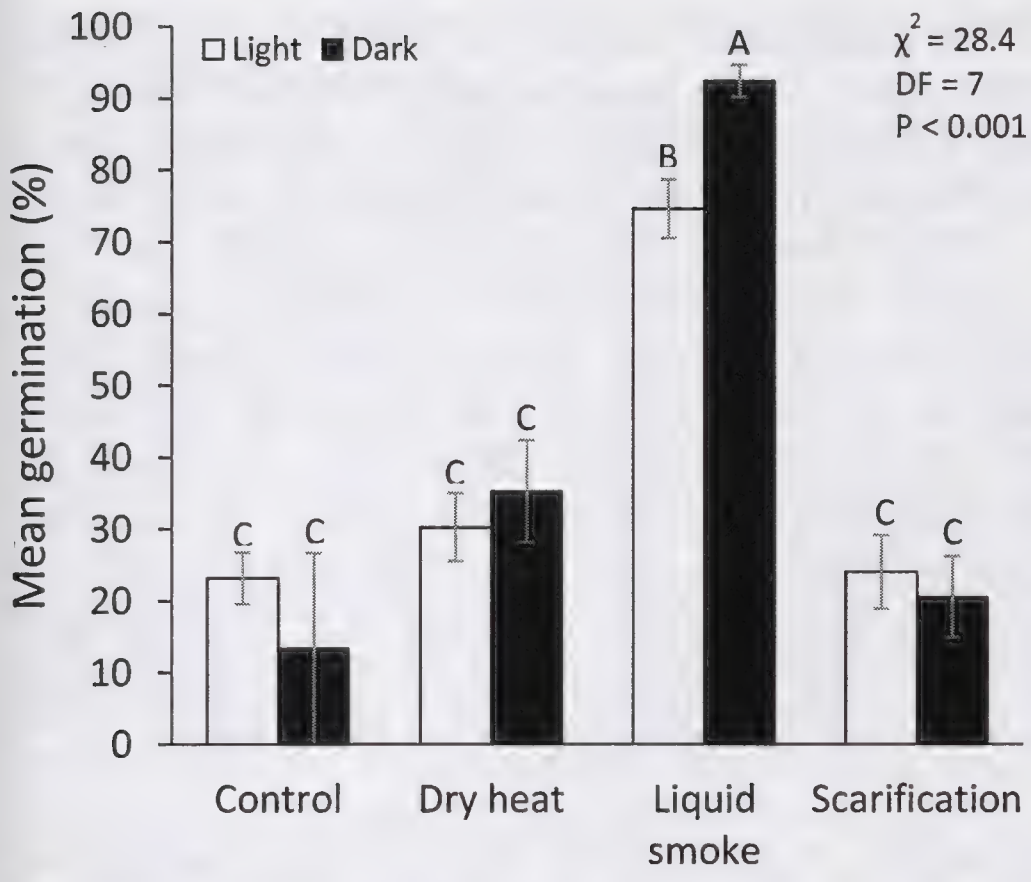

FIG. 3. Differences between mean germination rates by treatment under light and dark conditions. Physical and light treatments were analyzed together as a single combined treatment (e.g., Control/Light or Control/Dark). The hot soak treatment was excluded from analyses. Significant differences between treatment combinations were determined using $\alpha = 0.05$. Treatments that do not share a common letter are significantly different from one another. The error bars represent standard error.

microscope, including seeds in the hot soak treatment, in which no seeds germinated. Of the 77 hot soaked seeds that were cut, 51 were filled, 5 were empty and 21 were moldy.

A full factorial ANOVA to assess germination rates based on the cut test results detected significant differences in germination rates of potentially viable seeds by treatment (Table 2). This analysis showed that only physical treatments impacted the germination of potentially viable seeds. Neither the effect of the light treatment nor the interaction between the physical and light treatments was statistically significant overall. Similar to the observed germination rates, seeds treated with liquid smoke exhibited the highest germination rates of any other physical treatment (Table 3). Other treatments did not differ significantly.

Number of Days to First Germination

Physical and light treatments combined. The number of days between when seeds were placed in

TABLE 2. ANOVA TABLE FOR ANALYSIS OF GERMINATION RATES OF SEEDS BASED ON CUT TESTS. Significant effects were determined using $\alpha = 0.05$ and are denoted with an asterisk (*).

Source	DF	F-ratio	P-value
Model	7	6.1	0.0104*
Error	8		
Physical treatment	3	13.3	0.0018*
Light treatment	1	0.016	0.9013
Physical x light treatment	3	0.92	0.4753

TABLE 3. MEANS AND STANDARD DEVIATIONS OF GERMINATION RATES BY PHYSICAL TREATMENT BASED ON CUT TESTS. Treatments with overlapping 95% confidence intervals (CI) are not significantly different.

Treatment	Mean germination rate (%)	Standard deviation	Lower 95% CI	Upper 95% CI
Control	22.5	9.0	2.6	42.4
Dry heat	29.9	8.5	10.0	49.8
Liquid smoke	88.2	11.7	68.3	108
Scarification	24.5	17.9	4.6	44.4

Petri dishes and when radicle emergence was first observed ranged from 22 to 48 d. Seeds in the liquid smoke/dark and control/dark treatments germinated significantly faster than all other treatments, with first radicle emergence observed after 22 d (Fig. 4).

Effects of light treatments within physical treatment. The impacts of light on the speed of germination varied between treatments (Table 4). When evaluating the effect of light treatment within the control treatment (i.e., light vs. dark within the control treatment), we found no significant difference in the number of days to first germination (χ^2=2.3, df=1, P=0.1266), although the replication for control/dark was reduced due to an equipment malfunction. Similarly, light did not have a significant impact on germination in the dry heat treatment (χ^2=0.17, df=1, P=0.6775). However, seeds that received the liquid smoke treatment germinated an average of nine days earlier when subjected to dark compared to light conditions (χ^2=7.5, df=1, P=0.0062) and scarified seeds germinated more than 11 d sooner when subjected to dark versus light conditions (χ^2=5.7, df=1, P=0.0169).

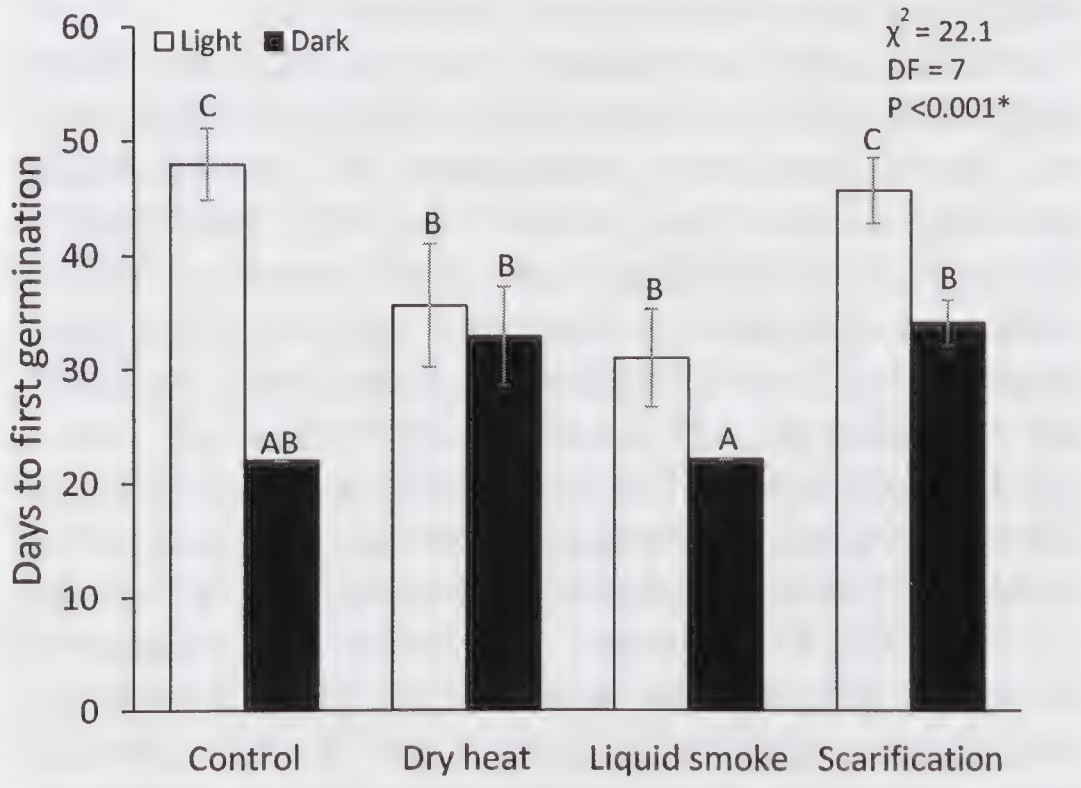

FIG. 4. Differences in mean number of days to first germination were assessed by treatment. Physical and light treatments were analyzed together as a combined treatment (e.g., Control/Light, Control/Dark, etc.). Significant differences between combined treatments were determined using $\alpha = 0.05$. Treatments that do not share a letter in common are significantly different from one another. The error bars for each treatment represent standard error.

TABLE 4. DIFFERENCES IN MEAN DAYS TO FIRST GERMINATION BETWEEN LIGHT TREATMENTS WITHIN PHYSICAL TREATMENTS. Significant differences between light and dark treatments within each physical treatment were determined using $\alpha = 0.05$ and are denoted with an asterisk (*).

	Mean days to first germination by light treatment		
Treatment	*Light*	*Dark*	P-value
Control	48.0	22.0	0.1266
Dry heat	35.7	33.0	0.6775
Liquid smoke	31.0	22.0	0.0062*
Scarification	45.7	34.0	0.0169*

Significance of results

Our results indicate that germination of *E. capitatum* seeds is smoke-stimulated. Seeds germinated at higher rates and more quickly when treated with liquid smoke and germinated under dark conditions compared to other treatment combinations. While a portion of seeds germinated across all treatments (aside from hot soak), suggesting that all seeds are not dormant, germination rates in the liquid smoke/dark treatment was nearly three times greater than those in the next best treatment (dry heat). Even under light conditions, exposure to liquid smoke more than doubled germination rates compared to seeds treated with dry heat. These results are congruent with previous findings in *E. crassifolium*, where a smoke treatment significantly increased germination compared to controls (Keeley 2005). Our results suggest that *E. capitatum* seed germination may be regulated by a chemical dormancy mechanism that is broken when the seeds are exposed to charate following a burn, although our study did not test the specific mechanism by which the liquid smoke treatment stimulated germination.

Ecologically, our findings suggest that fire likely plays an important role in the life cycle of *E. capitatum*, via smoke-induced germination of an otherwise partially-dormant seedbank. Given that low genetic diversity may contribute to reduced seed set (Elam 1994), it is possible that exposure to fire could trigger germination from an existing soil seed bank, facilitating the addition of novel genetics into the above ground community. Previous research has shown that fire can also stimulate seed set in multiple ways. For example, a study conducted in Florida, USA, focused on seed bank responses following disturbance in *Bonamia grandiflora,* a rare perennial herb that reproduces vegetatively and has low genetic diversity and seedling recruitment rates (Hartnett and Richardson 1989; Romano 1999). The results showed that new stem production, new genet recruitment (i.e., new seedlings), and seed production (via increased flowering) were significantly greater in burned sites compared to unburned sites (Hartnett and Richardson 1989). However, this study did not assess the mechanism by which seed germination was stimulated.

The significant impact of darkness on seed germination in the liquid smoke treatment (but not other treatments) suggests that *E. capitatum* seeds may benefit from seed burial, especially in the event of a fire. Previous research has noted that the vegetative reproduction of *E. capitatum* appears to show a strong response to disturbance (Wells 1962; Jacks et al. 1984) and gaps in chaparral vegetation (H. Schneider, personal observation), potentially indicating that individual new ramets thrive with increased light exposure. This two-pronged mechanism for reproduction (asexual and sexual) may represent a bet-hedging strategy to ensure or prolong aboveground persistence between fire events.

Limitations to the Current Study and Opportunities for Future Research

Despite the strong evidence for smoke-induced germination provided here, there are some limitations to our study. One perceived limitation is that we only collected seeds from one of the seven extant *E. capitatum* occurrences. However, a combination of our field work and previous observations suggest that *E. capitatum* only reliably produces seeds at one site (Elam 1994), so our opportunities for seed collections were limited. Furthermore, it is unlikely that germination cues would vary strongly between populations within a species with such a narrow geographic distribution.

Another potential limitation of the study is the lack of a combination dry heat/liquid smoke treatment. However, the relatively high germination rates that we observed in the liquid smoke treatment (>90%) compared to the others is a strong indicator that smoke is the primary mechanism for stimulating germination. An equipment malfunction midway through germination scoring led to a reduction in replication, especially in the control/dark treatment. This could have affected some of our statistical analyses, although it does not change our finding that seeds had a strong positive response to the liquid smoke treatment.

Finally, the complete absence of germination in the hot soak treatment suggests that the seeds were either damaged or killed by the treatment, although the damage was not readily apparent under the microscope, as most seeds appeared healthy and viable via visual inspection. Given that the duration of the soaking period was similar to that of seeds receiving the liquid smoke treatment, it is likely that the boiling water was too hot and negatively impacted the seeds. The same hot soak treatment has been implemented to stimulate germination in other California native plants (Emery 1988), including *Sanicula maritima* (Schneider unpublished data 2017), and other taxa such as *Acacia auriculiformis* (Khasa 1993), and it is likely that the seed coat of *E. capitatum* seeds is not thick enough to withstand exposure to boiling water. Additional study would be

required to determine why the hot soak treatment prevented germination.

To adequately address the threats to rare plants, the ecology of individual rare plant taxa must be better understood. In the case of *E. capitatum*, a return to the local to regional historic fire regime is unlikely, creating a need to develop and test alternative management strategies. Future research goals for *E. capitatum* include conducting field experiments aimed at measuring recruitment responses to treatments such as small-scale burns, irrigation with smoke water at the plot level, physical disturbance to the soil surface, a reduction in canopy cover of chaparral vegetation, or a combination of these treatments. In populations that are uniclonal or low in genetic diversity, outplanting novel genotypes is another way to try to facilitate viable seed production. Pollination experiments under controlled conditions would represent a first step in understanding whether increased genetic diversity within populations is likely to elicit increased seed production, as well as whether certain crosses are more successful than others. If field-based germination studies are successful, a deeper understanding of barriers to establishment will be needed to ensure that seedlings recruit into the reproductive stage.

Conservation and Management Implications

Our results suggest that the life cycle of *E. capitatum* is reliant upon fire at an unknown interval. Specifically, seed germination is maximized following exposure to smoke. Further investigation into the specific chemical compounds related to the effects of fire on germination were not included in this study. Our results can be directly applied to conservation and restoration efforts by facilitating increased production of plants. Historically, *E. capitatum* plants have been propagated vegetatively, which risks damage to the parent plant. Our findings can also be applied to the management of wild populations. For example, field observations in sites that have not recently burned suggest that recruitment from the seed bank is minimal (H. Schneider personal observation), but the application of fire as a management tool is fraught with complex natural, political and social challenges.

If, as our data suggest, fire plays an important role in the early part of the life cycle of *E. capitatum*, then the reintroduction of fire to the ecosystem could be an important part of an integrated conservation and adaptive management strategy. The final rule listing *E. capitatum* as federally endangered included altered fire regimes as one of the primary threats to the species (USFWS 2000). Based on available CalFire datasets dating back to 1878, it appears that only one of the occurrences has experienced fire in the last 150 yr (SB Atlas 2020) and that occurrence was found to be uniclonal (Elam 1994) and no seedlings were observed at the site following fire (Jacks et al. 1985). These data and observations suggest that germination from the seed bank has not been stimulated by fire at any extant occurrence in at least the last century and a half and that prescribed burning could be warranted. However, the fact that *E. capitatum* occurs predominantly on private and military land makes this type of management more complicated, as the plants co-occur with valuable human infrastructure. That said, controlled burns have been previously utilized as a tool for habitat management and fuels reduction at Vandenberg Air Force Base (Hickson 1988), and The Nature Conservancy's Dangermond Preserve is another location where prescribed fire may be considered a viable tool.

On the landscape scale, the challenges to the conservation and management of fire-adapted plants are exacerbated by the anthropogenic disruption of natural fire regimes. In the USA, organized fire suppression efforts have been implemented since the beginning of the 20th century in response to concerns related to forest protection, flood cycles, erosion, and property damage (Minnich 1987; Goforth et al. 2005). This suppression has potentially contributed to altered fire frequencies, increased coarse-scale patch structure, and large megafires in some chaparral ecosystems (Minnich and Chou 1997; Goforth and Minnich 2007). However, patterns observed in the 21st century suggest that fires in the shrub-dominated western portions of California, including the geographic range of *E. capitatum*, have often been wind-driven (Keeley and Syphard 2019) as opposed to being driven by increased fuel loads due to suppression. These wind-driven fires have the ability to burn across large swaths of habitat, despite extensive local fire histories and a lack of large fuel accumulations (Keeley and Syphard 2019).

Additionally, concurrent to fire suppression efforts, there has been an increase in anthropogenic impacts to chaparral landscapes, with urban growth leading to habitat loss and fragmentation, as well as increased human-caused ignitions. And, although many chaparral species are adapted to fire, increased frequency and anthropogenic modifications of fire regimes can result in drastic shifts in vegetation structure, composition, and biodiversity, while also threatening the persistence of fire-dependent flora (Hessl and Spackman 1995; Ames et al. 2017; Andela et al. 2017; Syphard et al. 2018). In addition to impacting species-specific ties to fire, fire suppression efforts at the landscape scale can alter succession and consequently reduce open habitat, inhibit obligatory sprouting and germination cues, and affect plant pathogen growth rates (Hessl and Spackman 1995; Schwartz et al. 1995). This is especially the case for *E. capitatum*, where lack of fire disturbance both hinders vegetative sprouting into open habitat and also precludes an important germination cue. Conversely, shorter than normal fire frequency intervals can hinder shrub recruitment of non-sprouting, obligate seeding species that may require multiple decades to fully establish (Zedler et al. 1983; Odion and Tyler 2002). Lower shrub recruitment, particu-

larly in frequently disturbed areas adjacent to established invasive plant populations, can increase the probability of type conversion to non-native grassland and consequently further exacerbate a system's susceptibility to fire (D'Antonio and Vitousek 1992; Keeley et al. 2011a; Keeley and Brennan 2012). These alterations to natural fire regimes, vegetation communities, and competitive interactions could significantly impact the life cycles of fire-adapted rare plants and decrease the odds of persistence on the landscape.

In an era of increasing environmental change, altered fire regimes represent just one example of how changes to landscape level processes and other anthropogenic disturbances are affecting rare plants. Other landscape level impacts such as altered hydrology due to anthropogenic activity (Kofron et al. 2019a) and sea level rise due to climate change (Berlin et al. 2012) also threaten the persistence of endangered plants in wild populations. As anthropogenic and climate change impacts increase, conservationists and land managers will continue to be challenged by how to mitigate for the alteration of landscape level processes, such as natural fire regimes and hydrological processes, as well as how to restore habitat to maintain ecosystem function and composition. Our germination study not only highlights the role that fire plays in the life history of *E. capitatum*, but also serves as a reminder of the importance of the effective maintenance and management of landscape level processes in wildlands. In the absence of natural fire regimes, fire-adapted rare plant populations may not be self-sustaining. Researchers, conservationists and land managers must endeavor to understand the life cycle of rare plants, including germination, to effectively manage for their long-term persistence in the wild. Although rare plants are uncommon on the landscape, they can act as canaries in the coal mine – signaling changes in natural processes that could have negative impacts at the community or ecosystem scale. Thus, understanding responses of rare plants to fire not only advances their conservation directly, but can also inform community-level conservation and restoration.

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PHYTOPHTHORA RAMORUM FOLIAR INFECTION REDUCES LEAF-LEVEL PRODUCTIVITY IN TANOAK AND CALIFORNIA BAY: A PILOT STUDY FROM REDWOOD NATIONAL PARK

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ABSTRACT

Woody plant infections of the pathogenic oomycete *Phytophthora ramorum* Werres, DeCock, & Manin'tVeld have brought an uncertainty to the future of western forests. Two understory hardwoods, tanoak (*Notholithocarpus densiflorus* (Hook. and Arn.) Manos, C.H.Cannon, and S.Oh) and California bay (*Umbellularia californica* (Hook. & Arn.) Nutt.), are commonly infected with *P. ramorum* leaf infection, the nonfatal foliar form of this pathogen. As the fatal bole infection form of this pathogen is most commonly studied, comparatively little research has been conducted on the nonfatal foliar infection form. This study measured physiological characteristics (midday water potential, stomatal conductance, net photosynthesis, and water-use efficiency) of healthy and infected foliage from tanoak and California bay trees in Redwood National Park to determine the effects *P. ramorum* foliar infection on leaf-level productivity. For both species, midday water potential, stomatal conductance, and net photosynthesis were all lower in infected samples compared to healthy samples. There was no significant difference in instantaneous water-use efficiency between infected and healthy foliage. Results suggest that *P. ramorum* leaf infection can lower leaf-level productivity and water status. Further research on the subject is still needed to better support informed management decisions in infected forests and to predict the long-term effects of *P. ramorum* leaf infections across a diverse suite of host species in the Pacific Northwest.

Key Words: hardwoods, leaf blight, net photosynthesis, physiology, stomatal conductance, sudden oak death, water potential, water-use efficiency.

Forests are experiencing large-scale mortality events worldwide (Allen et al. 2010). In the western U.S., increases in drought frequency and severity (Williams et al. 2012), forest vulnerability to pathogens (Simler-Williamson et al. 2019), and wildfire size and severity (Abatzoglou and Williams 2016) pose substantial challenges for the perpetuation of healthy forests. In California, drought-stressed forests are becoming increasingly vulnerable to attackers, such as bark beetles, resulting in widespread tree mortality across large areas of the state (Fettig et al. 2019).

In the 1990's, Marin County in northern California began experiencing massive tanoak (*Notholithocarpus densiflorus* (Hook. and Arn.) Manos, C.H.Cannon, and S.Oh) die-off, the cause of which was not determined until 2000 (Goheen et al. 2006). *Phytophthora ramorum* Werres, deCock, & Man in't Veld, an oomycete (water mold) pathogen that infects *Rhododendron* species in nurseries, was identified as the infectious agent causing extensive mortality in tanoak and true oaks (*Quercus* spp.). This pathogen can infect stems and branches with cankers which will eventually girdle and kill the host plant (this fatal form of the pathogen is often called "sudden oak death"). Additionally, *P. ramorum* can nonfatally infect foliage in over 100 species (Parke and Rizzo 2011) with a variety of manifestations (a form of the pathogen sometimes referred to as "ramorum leaf blight"). Since *P. ramorum* was identified, it has spread quickly and now exists in every coastal county in California north of Monterey, as well as in Curry County in southern Oregon (Kliejunas 2010; Cunniffe et al. 2106).

The pathogen appears to spread most easily in warm, wet spring conditions, so continued warming trends in northern California could accelerate a range expansion for *P. ramorum* (Rizzo and Garbelotto 2003). Climate research projects hotter temperatures, particularly in winter, and drier summers in the

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future (Mote et al. 1999; Mote 2003; Mote et al. 2003). As such, adaptive management to perpetuate forests in the face of extensive drought-induced tree mortality has become a widespread goal in the western U.S. (Millar et al. 2007). Furthermore, drier summers, coupled with fire suppression, have led to an increase in high-severity fires, posing an additional threat to western forests (Holden et al. 2018). These changes in climate, pathogen dispersal, and fire activity increase the vulnerability of California forests to pathogens and mortality and complicate resource management, which could have cascading negative effects on ecosystem services.

In California and Oregon, tanoaks provide important cultural, economic, and ecological benefits. Tanoak ranges from southern California to southern Oregon and although not a true oak, it plays an important role in many ecosystems by providing thermal cover, nesting habitat, and refuge for many wildlife species (Fryer 2008). Tanoaks are also an important food source for wildlife and indigenous people, particularly in redwood-dominated forests where they are one of the heaviest acorn producers of all oak species in the Pacific Northwest (Bowcutt 2015). Within Fagaceae, tanoak is unique because it is susceptible to both leaf and stem *P. ramorum* infections. When tanoak leaves become infected with *P. ramorum*, they can self-infect the stem with the pathogen, causing fatal cankers; thus, any infection in tanoak leads to inevitable death (Gillman 2011). It is possible tanoaks may become extirpated from the redwood forest ecosystem due to a combination of prolific pathogen sporulation during increasingly frequent mild, wet winters and tanoak's unique ability to self-infect stems with cankers (Ramage 2011; Cobb et al. 2012).

California bay (*Umbellularia californica* (Hook. & Arn.) Nutt.) is another evergreen hardwood that ranges from southern California to southern Oregon, an area roughly encompassing the tanoak range (Harnik et al. 2004). This hardwood produces olive-like fruits that are eaten by many small mammals and has aromatic foliage used by Native Americans for numerous cultural purposes (Stuart and Sawyer 2001). Contributing to the seemingly assured decline of tanoak, California bay is not susceptible to *P. ramorum* fatal stem infections, but its leaves are susceptible to infection and support remarkably high rates of pathogen sporulation, such that it is arguably the most virulent *P. ramorum* vector (Swiecki and Bernhardt 2008; DiLeo et al. 2009). Furthermore, efforts to eradicate California bay from infected areas have been minimally effective, highlighting the potentially pervasive influence that this foliar host and vector may have throughout its range (Valachovic et al. 2008). Research about the effects of *P. ramorum* on forest stand dynamics suggests that California bay may become more prominent in the wake of extensive tanoak mortality (Maloney et al. 2005). Speculatively, if tanoak were to become extirpated from the redwood forest ecosystem and California bay were to fulfill this vacated niche, the ecosystem effects of tanoak mortality related to *P. ramorum* may be somewhat buffered by the fact that California bay also produces a nutritious fruit.

Because *P. ramorum* stem infections are fatal and leaf infections are not, most research has focused on the former, leading to an extensive understanding of how stem cankers affect trees and comparably little knowledge about the effects of leaf infections on host species. Many studies specific to *P. ramorum* leaf infections have focused on nursery plants (Parke et al. 2004; Linderman et al. 2006). While these investigations can provide useful insights about the pathogen, they are limited in their ability to inform on the influence of the pathogen on native plants in the natural environment. In *Rhododendron macrophyllum* D.Don ex G.Don, artificial inoculation of foliage with *P. ramorum* can significantly decrease water supply capacity, stomatal conductance, and photosynthetic rate (Manter et al. 2007). Similarly, artificial inoculation of California bay foliage with *P. ramorum* significantly decreased photosynthetic efficiency (DiLeo et al. 2009). If these responses are also true for naturally inoculated forests with numerous foliar host species, these leaf-level effects on physiology could influence forest productivity on a large scale. Additionally, reduction in photosynthetic capacity due to *P. ramorum* foliar infection may decrease resources for resistance against drought and secondary pathogens, which could affect overall forest health (Fichtner et al. 1995). As *P. ramorum* continues to spread, improved understanding of the effects of foliar infections will strengthen efforts to effectively manage the pathogen and infected forests.

This study focuses on California bay and tanoak within Tall Trees Grove of Redwood National Park. Since the discovery that *P. ramorum* can spread through waterways, it has been identified in Redwood Creek, a first-order watercourse that runs along a trail in the study area (Valachovic and Kanode Rice 2012; Eyre and Garbelotto 2015). Large patches of tanoak and California bay within this grove have become heavily infected with *P. ramorum* leaf infections, and some tanoaks are showing symptoms of stem infections. Given the abundance of foliar hosts that can survive with this pathogen indefinitely, we were curious about the effects of *P. ramorum* on leaf water potential (Ψ), stomatal conductance of water vapor (g_s), net photosynthetic capacity (P_{net}), and instantaneous water-use efficiency, $WUE = P_{net}/g_s$), as it would seem that foliar infections could alter host water status and gas exchange capacity and that these effects could be impactful when considered at the landscape scale across time. By comparing healthy and infected foliage from tanoak and California bay, the objective of this study was to quantify the physiological effects of *P. ramorum* leaf infections on host trees. We hypothesized that *P. ramorum* leaf infection would decrease Ψ, gas exchange capacity (g_s and P_{net}), and WUE.

Methods

Site Description

This study took place within Tall Trees Grove in Redwood National Park, CA (41°12′34.9″N, -124°00′40.1″W, 30 m elevation), located nine km south-southeast of Orick, CA and eight km east of the Pacific Ocean. The 30-year average annual climate for Tall Trees Grove was consistent with the temperate rainforest biome description per the PRISM Climate Group, (Oregon State University, http://prism.oregonstate.edu, created 11 July 2012 created) ($t_{min} = 6.58 \pm 0.12°$ C, $t_{mean} = 12.37 \pm 0.10°$ C, $t_{max}18.16 \pm 0.11°$ C, ppt = 1774 ± 81 mm). Tall Trees Grove is an old-growth stand dominated by redwood (*Sequoia sempervirens* (D.Don) Endl.) and including Douglas-fir (*Pseudotsuga menziesii* (Mirab.) Franco), western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), California bay, tanoak, red alder (*Alnus rubra* Bong.), and bigleaf maple (*Acer macrophyllum* Pursh.) in the overstory. Dominant shrubs in the area include evergreen huckleberry (*Vaccinium ovatum* Pursh.), salmonberry (*Rubus spectabilis* Pursh.), salal (*Gaultheria shallon* Pursh.), and sword fern (*Polystichum munitum* (D. C. Eaton) Diels.). Of these species, coast redwood, Douglas-fir, California bay, tanoak, bigleaf maple, evergreen huckleberry, and salmonberry are known foliar hosts for *P. ramorum*, with tanoak being the only species capable of bole infections (Davidson et al. 2003).

Sampling & Data Collection

All sample trees were located within the floodplains of Redwood Creek and all measurements were conducted in the summer of 2019. The two most abundant hardwood species within Tall Trees Grove that are susceptible to *P. ramorum* foliar infection, tanoak and California bay, were analyzed to test the hypothesis that *P. ramorum* leaf infection reduces leaf-level productivity. Due to the high levels of *P. ramorum* infection at this location, it was not possible to find enough uninfected trees for comparison; this study therefore only included infected trees. Infected trees were found throughout the grove with varying levels of foliar infection (Fig. 1). Ten infected tanoak trees and ten infected California bay trees were selected for measurements. Infected tanoaks were identified by the presence of olive-brown leaves with blackish midribs, and infected California bay trees were identified by leaves with tip necrosis, pixelated chlorosis, and "yellow halo" margins between healthy and infected tissue (Fig. 2). Foliar infection was confirmed in the lab (see below). Because *P. ramorum* can infect tanoak leaves, twigs, branches, and boles, care was taken to select trees that only exhibited leaf infection symptoms and no to minimal twig infections; trees with signs of bole infection (i.e., cankers) were avoided. For all study trees, the following data were recorded: diameter at breast height (1.37 m, DBH), height, crown length, live crown ratio (crown length / tree height), canopy class, local competition of neighboring trees via basal area density measured with an angle gauge (JIM-GEM Cruz-All, basal area factor 40), and percent crown infected (Condeso and Meentemeyer 2007).

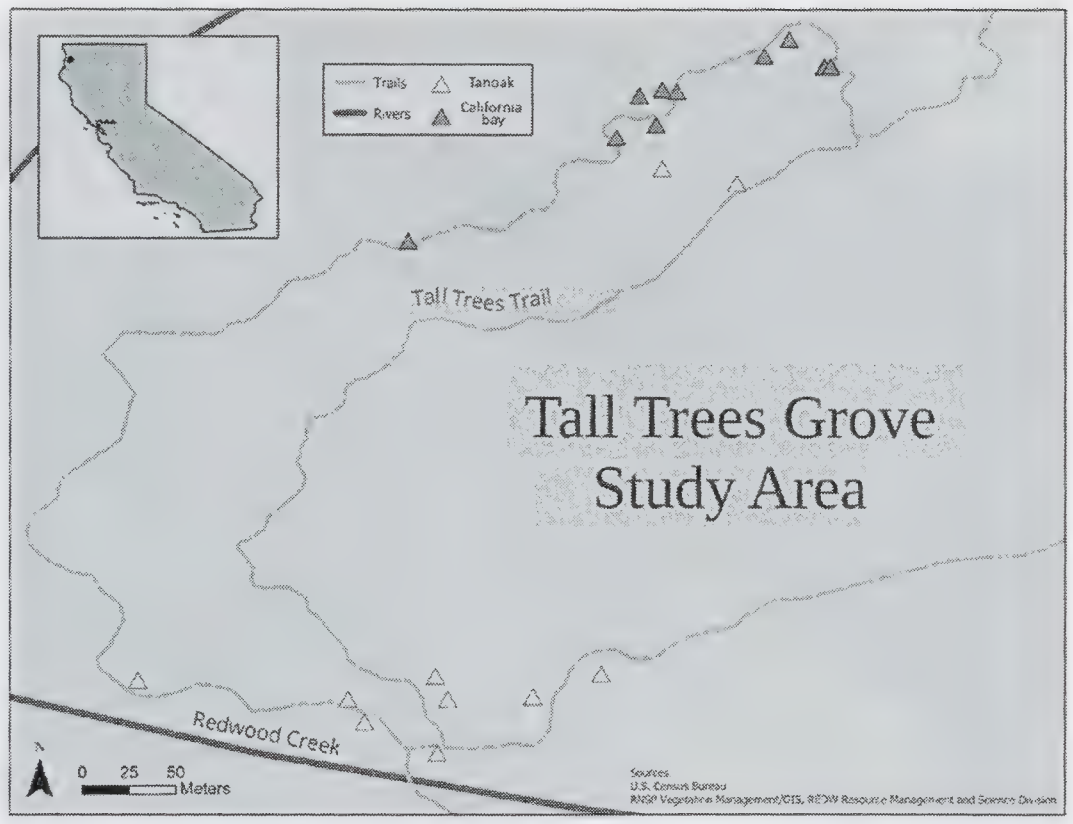

FIG. 1. Tanoak (white triangles) and California bay (green triangles) study trees at Tall Trees Grove, Redwood National Park, CA.

Physiological data collection included field- and lab-based measurements using healthy and infected branches. All branches were carefully chosen to maintain consistent canopy position (suppressed or intermediate) and presence or absence of symptoms. Field-based measurements of midday water potential (Ψ_{md}) were made on two comparable consecutive sunny days in July, a dry month in the middle of the growing season, from infected and healthy branches of each study tree using a pressure chamber (Model 600, PMS Instruments, Corvallis, OR). From each tree, multiple Ψ_{md} measurements were taken for each health class (healthy and infected) until three values within 0.1 MPa had been measured; these values were then averaged into a single value for each class. For lab-based measurements of gas exchange capacity, three healthy and three infected branches (approximately 15 cm in length) were collected from each study tree over the course of four weeks, from late June through July. Cut branches were then immediately re-cut under water, transported to the Forest Physiology Laboratory at Humboldt State University in florist tubes, and allowed to hydrate overnight.

Lab Analyses

After overnight equilibration, rates of net photosynthesis (P_{net}, mol CO_2 m^{-2} s^{-1}) and stomatal conductance of water vapor (g_s, μmol H_2O m^{-2} s^{-1}) were measured on hydrated cuttings under standardized, optimal conditions using a LI-6400 portable photosynthesis system (Li-Cor Inc., Lincoln, NE) with a 2 × 3 cm standard leaf chamber equipped with a red-blue LED source (model 6400-02B). For these measurements, the following settings were used:

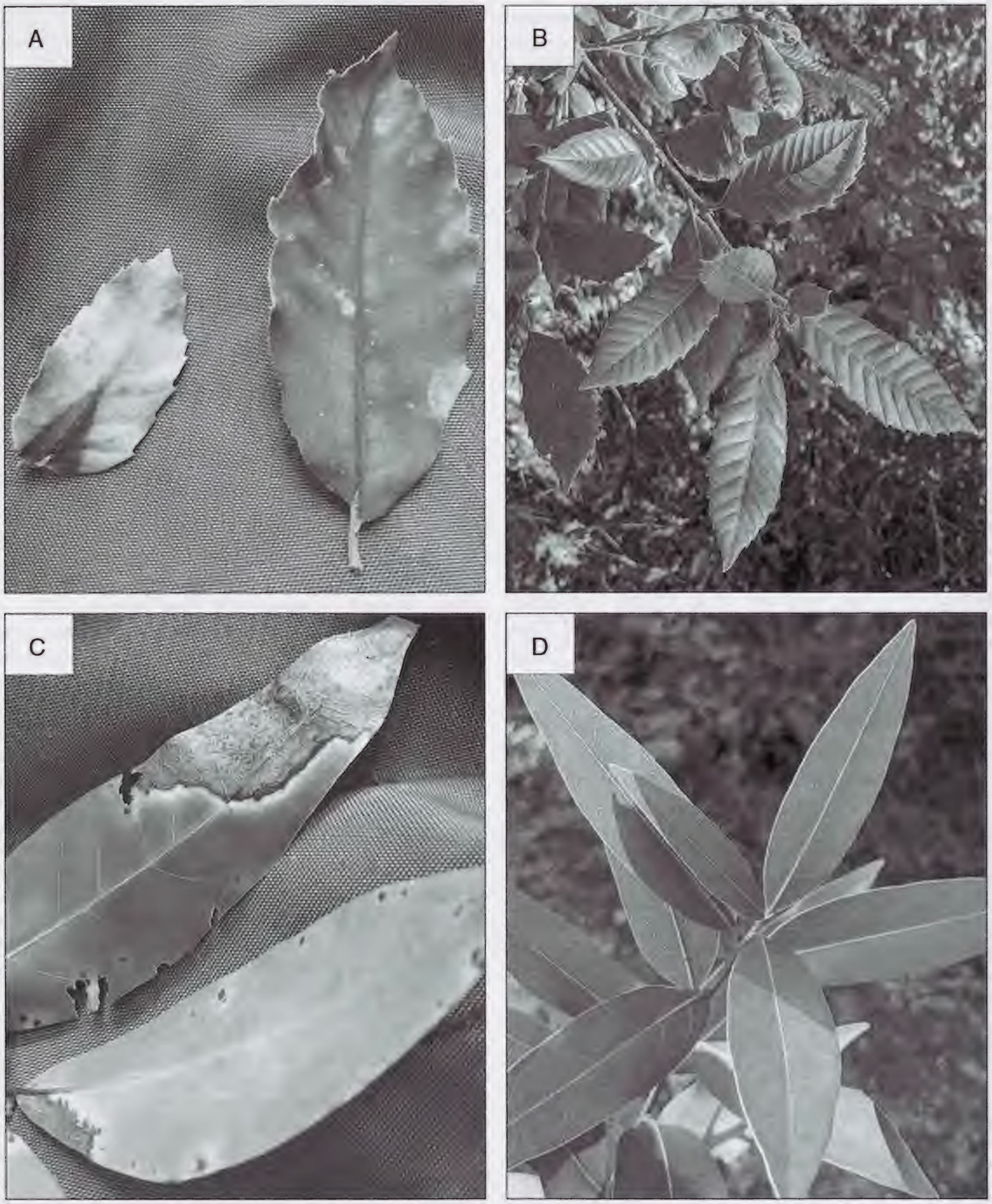

FIG. 2. A) Tanoak leaves infected with *Phytophthora ramorum* and showing symptoms such as brown coloring and darkened midribs, B) healthy tanoak leaves, C) California bay leaves infected with *P. ramorum* and showing symptoms such as tip necrosis, yellow halo at margin between infected and healthy tissue, and pixelated diseased spots, and D) healthy California bay leaves. Note that the infected tanoak examples shown here represent extreme cases.

reference $CO_2 = 400$ ppm, photosynthetically active radiation = 1600 μmol m^{-2} s^{-1}, and block temperature = 20° C. Per cutting, P_{net} and g_s were measured on one leaf; leaf measurements from the three cuttings of each health class were then averaged into single values for each tree. On infected cuttings, care was taken to select symptomatic leaves for the leaf chamber. For each leaf, water-use efficiency was calculated using these gas exchange measurements ($WUE = P_{net}/g_s$).

TABLE 1. SPECIES, MEANS OF DIAMETER AT BREAST HEIGHT (1.37 M, DBH), HEIGHT, CROWN LENGTH, LIVE CROWN RATIO (CROWN LENGTH / TREE HEIGHT X 100), CANOPY CLASS (CD = CODOMINANT, I = INTERMEDIATE, AND S = SUPPRESSED), LOCAL BASAL AREA DENSITY, AND DEGREE OF *PHYTOPHTHORA RAMORUM* LEAF INFECTION FOR TANOAK (N = 10 TREES) AND CALIFORNIA BAY (N = 10 TREES). Measurements were collected in Summer 2019 from Tall Trees Grove, CA.

Species	DBH (cm)	Height (m)	Crown Length (m)	Live Crown Ratio	Canopy Class	Basal Area (m^2 ha^{-1})	Degree Infected (%)
Tanoak	37.8	16.4	14.7	0.90	S	119	15
	19.5	10.0	6.3	0.63	S	101	35
	5.2	5.8	5.7	0.98	S	101	33
	13.0	13.5	11.2	0.83	S	119	8
	13.3	8.5	6.5	0.76	S	128	9
	15.6	12.3	12.0	0.98	S	119	5
	15.8	8.7	5.2	0.60	S	138	4
	18.0	15.5	8.6	0.55	I	110	30
	20.8	12.5	9.0	0.72	S	138	2
	14.5	10.8	10.0	0.93	S	110	2
California bay	32.6	13.5	11.0	0.81	I	83	80
	19.3	9.3	8.3	0.89	S	92	70
	16.2	6.2	5.1	0.83	S	110	70
	30.5	10.2	7.5	0.73	S	128	40
	25.9	13.2	9.9	0.75	S	119	65
	62.7	30.0	19.0	0.63	I	128	30
	64.7	8.7	4.7	0.54	S	110	65
	65.6	18.8	16.6	0.88	I	101	70
	41.7	20.1	15.6	0.77	CD	128	80
	34.5	9.1	5.7	0.63	I	119	70

Following gas exchange measurements, four hole-punch-sized samples (approximately 1 cm diameter) were taken from each cutting, placed in a "PARP-NH" medium (potato dextrose agar, clarified V8 juice, pimaricin, ampicillin, rifampin, PCNB, nystatin, and hymexazol, modified from Ferguson and Jeffers 1999), and incubated for approximately two weeks. They were then visually checked for signs of *P. ramorum* growth using a light microscope to determine whether the samples were indeed healthy or infected. A subsample identified as infected with *P. ramorum* was sent to the Plant Pest Diagnostics Lab at the California Department of Food and Agriculture for genetic confirmation using PCR and sequencing of the ITS region of ribosomal DNA. For tanoak, all infected limbs cultured positive for *P. ramorum* and no healthy limbs cultured positive for *P. ramorum*. From California bay trees, we were unable to culture *P. ramorum*, but it is notoriously difficult to culture leaves from this species, possibly due to their unique chemistry, particularly during the dry summer conditions under which we sampled when the pathogen might be relatively dormant (Chimento et al. 2012; Garbelotto and Hayden 2012; Hüberli et al. 2012). For California bay, we therefore based our assignment of healthy versus infected on visual symptoms (Fig. 2). Given that our health assignments based on visual symptoms for tanoak were all confirmed by microscope and genetic analysis (on a subsample), we feel confident that our California bay leaves were accurately classified as healthy or infected.

Statistical Analyses

All statistical analyses were done using JMP (version 16, SAS Institute, Cary, NC). One-way Analyses of Variance (ANOVAs) were used to compare tree-level characteristics (e.g., DBH, height) between tree species. Paired t-tests were used to compare physiology (Ψ_{md}, g_s, P_{net}, and WUE) between healthy and infected leaves sampled from the same trees. One-way ANOVA was also used to compare physiology between species. All analyses were based on a sample size of 10 trees per species.

RESULTS

Tree characteristics are summarized in Table 1. On average (± standard error), California bay trees had significantly larger DBH (39.37 ± 5.91 cm) compared to tanoaks (17.35 ± 2.65 cm, $P = 0.03$). Height ($P = 0.33$), live crown ratio ($P = 0.61$), and competition ($P = 0.34$), as measured by the basal area surrounding each study tree, did not significantly differ between species. Most trees were classified into suppressed and intermediate canopy classes, with one California bay in a codominant position. The degree of *P. ramorum* leaf infection was significantly higher in California bay (64 ± 5%) than in tanoak (14 ± 4%, $P < 0.001$). For tanoak, microscopic examination of leaf fragments allowed to grow on an agar culture for two weeks confirmed that healthy leaves were in fact uninfected and that infected leaves were in fact infected with *P. ramorum*. For California bay, we were unable to culture *P. ramorum* from leaf fragments, which is common with this species

TABLE 2. MEAN (± SE) MIDDAY WATER POTENTIAL (Ψ_{MD}), STOMATAL CONDUCTANCE TO WATER VAPOR RATE (G_S), NET PHOTOSYNTHETIC RATE (P_{NET}), AND WATER-USE EFFICIENCY ($WUE = P_{NET}/G_S$) FOR TANOAK (N = 10 TREES) AND CALIFORNIA BAY (N = 10 TREES). Samples were collected in Summer 2019 from Tall Trees Grove, CA. Measurements were made on healthy foliage and foliage infected with *Phytophthora ramorum*; Ψ_{md} was measured in the field, and g_s, P_{net}, and WUE measurements were taken in the lab on hydrated cuttings. Statistics (P-values and mean difference [MD]) from paired t-tests ($\alpha = 0.05$) comparing healthy and infected foliage are also provided.

	Ψ_{md} (MPa)		g_s (mol H_2O m^{-2} s^{-1})		P_{net} (μmol CO_2 m^{-2} s^{-1})		WUE (%)	
	Tanoak	California bay	Tanoak	California bay	Tanoak	California bay	Tanoak	California bay
Healthy	−0.62 (0.03)	−1.14 (0.14)	0.031 (0.010)	0.033 (0.004)	1.83 (0.30)	3.38 (0.41)	89 (8)	126 (28)
Infected	−0.76 (0.07)	−1.23 (0.11)	0.016 (0.004)	0.027 (0.003)	1.08 (0.22)	2.26 (0.27)	105 (16)	82 (8)
MD	0.15	0.09	0.015	0.006	0.75	1.12	−16	45
P-value	0.03	0.02	0.17	0.20	0.01	0.04	0.21	0.19

(Chimento et al. 2012; Garbelotto and Hayden 2012; Hüberli et al. 2012), so had to rely on visual assessments of health.

In both species, health status (infected with *P. ramorum* v. healthy) significantly affected leaf physiology (Table 2). We measured significantly lower Ψ_{md} in infected foliage compared to healthy foliage in tanoak ($P = 0.03$) and California bay ($P = 0.02$, Fig. 3A). Similarly, we measured reduced g_s in infected foliage compared to healthy foliage in both species, although this trend was not significant for tanoak ($P = 0.17$) or California bay ($P = 0.20$, Fig. 3B). We measured significantly lower P_{net} in infected foliage compared to healthy foliage in tanoak ($P = 0.01$) and California bay ($P = 0.04$, Fig. 3C). Notably, tanoak infected foliage had a 45 ± 12% reduction in P_{net} compared to healthy foliage and in California bay, infected foliage had a 33 ± 19% reduction in P_{net} compared to healthy foliage. Water-use efficiency (P_{net}/g_s) did not significantly differ between healthy and infected foliage in tanoak ($P = 0.21$) or California bay ($P = 0.19$, Fig. 3D).

DISCUSSION

The purpose of this study was to determine the physiological effects of *P. ramorum* leaf infection on tanoak and California bay foliage. For this investi-

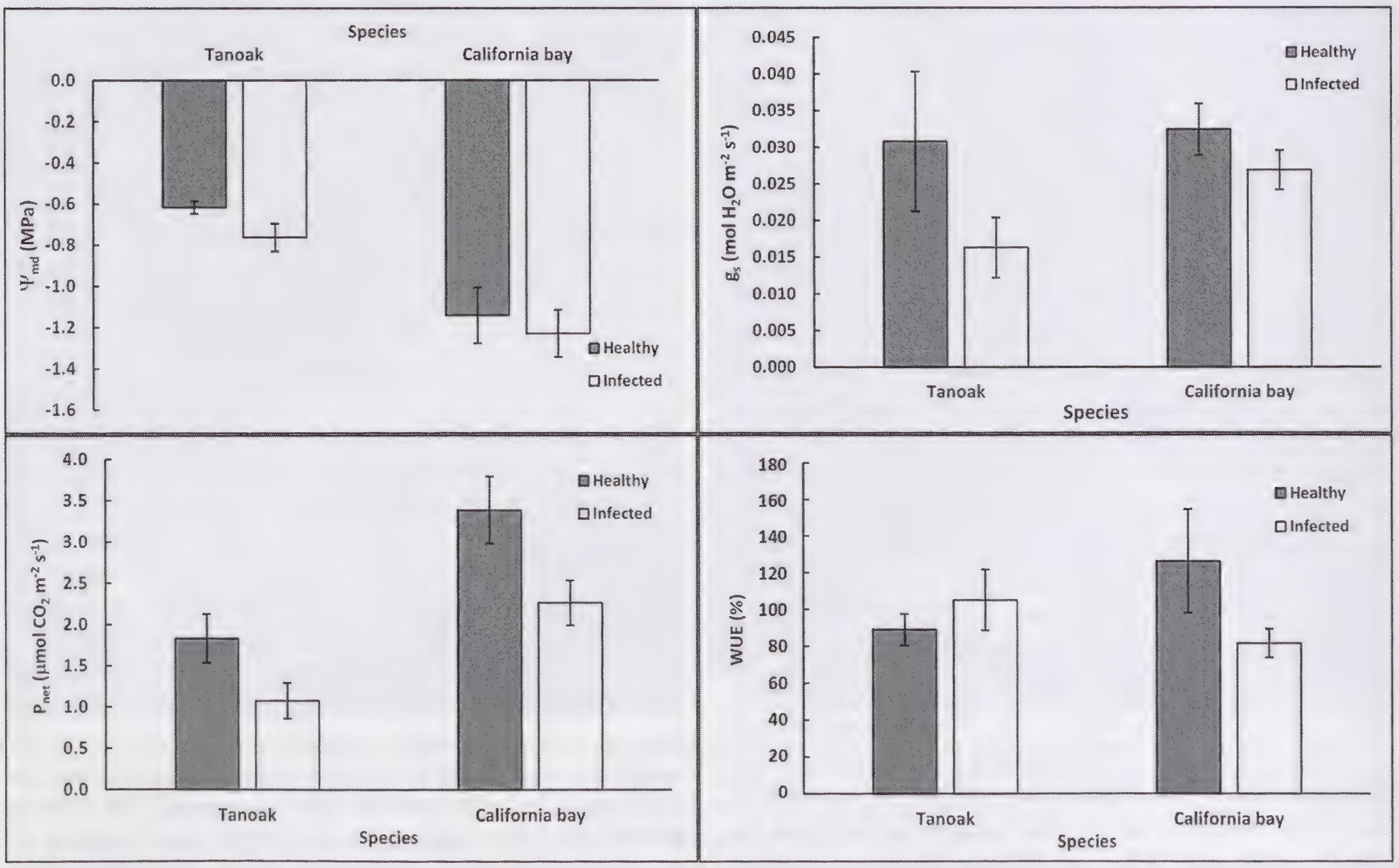

FIG. 3. Tanoak and California bay mean (± SE) A) midday water potential (Ψ_{md}), B) stomatal conductance (g_s), C) net photosynthetic rate (P_{net}), and D) water-use efficiency ($WUE = P_{net}/g_s$) for healthy foliage (grey) and foliage infected with *Phytophthora ramorum* (white). All measurements were made during the 2019 summer months on samples collected from Tall Trees Grove, CA. Midday Ψ was measured in the field and g_s, P_{net}, and WUE were measured on hydrated cuttings in the laboratory. Within each species, health statuses not sharing the same lowercase letter are significantly different; within a health status, species not sharing the same uppercase letter are significantly different (n = 10 trees per species; $\alpha = 0.05$).

gation, we used four physiological metrics that can provide information on tree vigor and health: midday water potential (Ψ_{md}), stomatal conductance (g_s), net photosynthesis (P_{net}), and water-use efficiency ($WUE = P_{net}/g_s$). While Ψ_{md} represents a plant's maximum daily water stress, g_s, P_{net}, and WUE are measures of leaf gas exchange. In both species, *P. ramorum* leaf infection lowered Ψ_{md}, g_s, and P_{net}, indicating that infected foliage experiences greater water stress and reduced gas exchange compared to healthy foliage. We note that these physiological effects of leaf infection may be even more pronounced if compared against healthy foliage from uninfected trees, but this was not possible in our study due to a lack of uninfected trees. We also note that because only tanoak trees without *P. ramorum* bole infection were included in this study, these trees were inherently only recently infected. As such, it follows that we found higher rates of infection in California bay trees compared to tanoaks. Further investigation is needed to determine if/how the physiological effects of *P. ramorum* leaf infection vary with time-since-infection.

As decreased P_{net} can result from reduced gross photosynthesis and/or increased respiratory costs, we speculate that, in infected foliage, reduced stomatal conductance lowered gross photosynthesis while elicitin-induced cell death increased respiration (Fichtner et al. 1995; Hayden et al. 2014). Because long-term decreases in P_{net} can ultimately diminish growth rates and carbon storage (Fichtner et al. 1995), these findings suggest that foliar hosts likely suffer reduced productivity. Reductions in P_{net} due to foliar infection could therefore have substantial implications for heavily infected stands in terms of stand-level water use, health, productivity, carbon sequestration, and carbon storage. Foliar *P. ramorum* infection might also reduce leaf life expectancy, as California bay tends to drop infected foliage earlier than healthy foliage (Davidson et al. 2005); this increase in leaf production could potentially increase respiration costs. Further, because these lab-based findings of reduced gas exchange in infected foliage were made on hydrated cuttings, we speculate that *in situ*, these trends may be even more pronounced, as field-based measurements found lower Ψ_{md} in infected foliage compared to healthy foliage and Ψ is typically positively correlated with gas exchange (Martinez-Vilalta & Garcia-Forner 2018). Specifically, we expect that field-based measurements of *in situ* g_s would show a greater reduction in infected foliage compared to healthy foliage than the reduction we observed using hydrated cuttings.

Interestingly, although P_{net} and g_s were both reduced in infected foliage compared to healthy foliage, WUE (P_{net}/g_s) did not vary between health statuses in either species. This stability in WUE suggests that infection induced similar magnitudes of reduction in CO_2 assimilation rate and water transpiration rate, indicating a possible homeostatic maintenance of water use in these species (McDowell et al. 2006). Despite stable WUE, our findings suggest that infected trees experience increased water stress and reduced gas exchange capacity; this added water stress due to infection would have larger long-term impacts on California bay, given that infected tanoaks will die due to eventual bole infection (Gillman 2011). Reductions in plant water status related to *P. ramorum* leaf infection could become increasingly impactful, as forest mortality due to hotter and drier droughts is a current problem affecting many western forests (Mote et al. 2003; Williams et al. 2010, 2012). Moreover, it is likely that reductions in water status and carbon assimilation resulting from *P. ramorum* leaf infection could lower tree resistance to secondary pathogens, further exacerbating the effects of leaf infection (Kozlowski et al. 1991). In tanoaks, increased vulnerability to secondary pathogens (e.g., ambrosia beetles [*Monarthrum scutellare* LeConte], oak bark beetles [*Pseudopityophthorus pubipennis* LeConte], and sapwood rotting fungi [*Hypoxylon thouarsianum* (Lév.) Y.M. Ju, J.D. Rogers & H.M. Hsieh]) has the potential to speed the eventual death related to bole infection (Rizzo and Garbelotto 2003). Although the California bay is not vulnerable to any serious insect pests, heightened vulnerability from *P. ramorum* leaf infections could lower overall long-term tree vigor via increased infections of oak bark beetles (*Pseudopityophthorus* spp.), powderpost beetles (*Ptilinus basalis* LeConte), heart rot fungi [*Ganoderma applanatum* (Pers.) Pat.], and root pathogens (*Armillaria* spp.) (Burns and Honkala 1990).

As climate continues to change, it is likely that *P. ramorum* will have an increasingly noticeable impact on forests. Increased tanoak mortality, as well as reduced vigor in a multitude of foliar hosts, could vastly alter species composition in ecosystems where the ranges of tanoak and California bay overlap. Due to prolific sporulation in California bay (Alexander and Swain 2003) and the broad range and diversity of other sporulating hosts (Goheen et al. 2006), tanoak and some true oaks are unlikely to escape infection and subsequent mortality from *P. ramorum* (Rizzo and Garbelotto 2003). Gaps resulting from large-scale oak and tanoak mortality have the capacity to alter stand dynamics (Brown and Allen-Diaz 2009), forest structure (Maloney et al. 2005), and species composition (Ramage et al. 2011; Metz et al. 2012). Although tanoak might be able to persist in forests as a sprouting shrub (Cobb et al. 2012), the potential gaps created by the extirpation of oaks and overstory tanoak will likely lead to an increase in California bay and other foliar carrier species immune to the lethal stem infecting form of *P. ramorum* (Maloney et al. 2005). Additionally, *P. ramorum*-created gaps could enhance seedling establishment for redwood, a species that primarily asexually regenerates via basal sprouts, as well as vacate habitat for deep-rooting, shade-tolerant trees; as such, it is possible that

overstory tanoak extirpation will alter forest structure (Ramage et al. 2011).

Widespread mortality of tanoak will likely have cascading effects on ecosystems and indigenous cultures (Crooks 2002). The acorns from tanoak are a vital food source for wildlife, and the tree provides habitat for important species such as Humboldt's flying squirrel (*Glaucomys oregonensis* Bachman), a keystone species of the Pacific Northwest that benefits trees by spreading truffles (mycorrhizal symbionts) through forests and serves as prey for higher trophic species (USDA NCRS 2003; Smith 2007; Arbogast et al. 2017). Tanoak is also an irreplaceable cultural component of many Native American tribes, including the Pomo, Karuk, and Hupa, whose ancestral lands lie within the tree's range (Bowcutt 2015). The loss of tanoak in these native lands would have catastrophic effects on tribal resources (USDA NCRS 2003; Bowcutt 2015). Informed and effective management of tanoak is therefore needed, given that trees from across this species' small range appear to be extremely susceptible to *P. ramorum*. As such, its survival likely depends on finding and propagating resistant genotypes and managing environmental factors as much as possible to be unfavorable to the pathogen (Hayden et al. 2011).

Seasonal shifts in temperature and moisture regimes associated with changing climate will likely amplify interactions and trends among *P. ramorum*, ecosystem management, and forest health (Venette and Cohen 2006; Eyre et al. 2013). Given the complex interactions among disturbances, it is important for management in infected areas to consider the myriad ways that *P. ramorum* can influence long-term forest dynamics and health. Thus far, efforts to eradicate California bay and intentionally establish other non-host, native species and/or genetically-resistant tanoaks offer potentially effective methods to help decrease *P. ramorum* spread (Ramage et al. 2011; Dodd et al. 2013), although the results are mixed (Valachovic et al. 2008, Valachovic et al. 2017).

As such, improved understanding about the effects of *P. ramorum* leaf infection could aid management decisions. This work demonstrates that *P. ramorum* leaf infection can significantly negatively impact host trees at the leaf-level. We note the limitations of this pilot study: our small sample size, our use of only two host species, and our use of only one study location. Nevertheless, we feel that our findings are compelling and inspire further investigation of this topic. To build on this work, future studies using larger sample sizes, more host species, and multiple locations could investigate how these leaf-level effects scale up to the whole tree- and stand-levels. Additionally, quantifying percent infected surface area of leaves used for gas exchange measurements could improve our understanding about the influences of foliar infection on leaf physiology. As *P. ramorum* continues to spread through the Pacific Northwest, a better understanding of the effects of *P. ramorum* leaf infection will be necessary for effective, long-term forest management.

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EVOLUTION OF THE CHOLLAS (CACTACEAE)

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ABSTRACT

Cacti with the common name cholla are classified into several genera of the subfamily Opuntioideae (Cactaceae), and appear to be a monophyletic group. Although recent studies have provided strong resolution of the base of this group, assessment of evolutionary processes within genera have been limited due to taxon sampling. Analysis of four spacer and intron sequences of the chloroplast genome reveals evolutionary patterns and trends that are largely congruent with other recent studies. We concur with recent calls for the recognition of *Micropuntia pulchella* as monotypic and distinct from *Grusonia*, the name we use to refer to all species sometimes classified under *Marenopuntia* and *Corynopuntia*. *Grusonia* is monophyletic, and *Cylindropuntia* is borne on two clades of differing branch lengths. By incorporating the elements of ploidy, reproduction, and sequence divergence, we provide new insight into allopolyploid ancestry, the adaptive impact of ploidal-level variation in species, and the role of reproductive mode in diversification rates in the chollas.

Key Words: *Cylindropuntia*, chloroplast DNA, *Grusonia*, phylogeny, polyploidy.

The common name cholla, in combination with a great range of adjectives (club, dwarf, pencil, jumping, etc.) has been applied to mat-forming, shrubby, to tree-like species of cacti with segmented, cylindrical stems in North America. They are a familiar feature of the Chihuahuan, Sonoran, and Mohave deserts, and vary in distribution from narrow endemics to species with ranges that span multiple states on both sides of the U.S.-Mexican border. And although recent work has included the chollas in broader analyses of cactus phylogeny and taxonomy, treatment of evolutionary trends and interspecific relationships in this group have been less common. The present study aims to add to our understanding of the natural history of the chollas.

Recent classifications of the 70 or so cholla species have distributed them among a variety of genera: *Cylindropuntia* (Engelm.) F.M.Knuth, *Corynopuntia* F.M.Knuth, *Grusonia* Rchb.f. ex Britton & Rose, *Marenopuntia* Backeberg, or *Micropuntia* Daston. Contemporary phylogenetic analyses portray the chollas as monophyletic within subfamily Opuntioideae (Griffith and Porter 2009). The work of Barcenas et al. (2011) and Ritz et al. (2012) generated a proposal for three tribes in the Opuntioideae: Opuntieae, Tephrocacteae, and Cylindropuntieae, the latter of which would include the traditional chollas plus *Pereskiopsis* Britton & Rose and *Quiabentia* Britton & Rose. Recent work also resolves this pattern (Majure et al. 2019; Köhler et al. 2020).

Cylindropuntia is the largest genus of chollas; it comprises approximately 40 species, displays the broadest geographic range, and its circumscription is not currently debated. *Cylindropuntia* species are distinguished from the other chollas primarily by smooth spines that are fully covered by deciduous, papery sheaths. The remaining chollas have at one extreme all been assigned to *Grusonia* Rchb.f. ex Britton & Rose (*sensu* Stuppy 2002) or split among *Grusonia*, *Corynopuntia*, *Marenopuntia*, and *Micropuntia* in various treatments. These species contrast with *Cylindropuntia* by exhibiting mostly flattened, rough spines, with a spine sheath lacking or covering just the tip of the spine. The history of taxonomic revisions involving chollas has been summarized elsewhere (Barcenas 2016).

Diversification of the chollas has been tied to the expansion of the deserts of North America and the climatic fluctuations of the Pleistocene epoch (Arakaki et al. 2011; Hernandez-Hernandez et al. 2014; Majure et al. 2019). Adaptation and speciation were likely facilitated by hybridization and polyploidy, both of which are common in the chollas (Pinkava 2002). Polyploidy, following hybridization (allopolyploidy) or not (autopolyploidy), has resulted in chromosome count variation among and sometimes within species of *Cylindropuntia* ranging from $2n = 22$ to 88 (Pinkava 2002).

Despite solid recent work revealing the main clades of the chollas, there is still need for resolution of the patterns within these clades, incorporating both diploid and polyploid species. In the present study, we assess sequence variation in spacer regions and introns of the chloroplast genome to provide phylogenetic insight. Prior work has shown the utility of non-coding chloroplast DNA to phylogenetic studies both across vascular plants (Shaw et al. 2005, 2007) and among cholla species specifically (Wallace and Dickie 2002; Griffith and Porter 2009;

Barcenas et al. 2011; Barcenas 2016). For the purposes of interpreting allopolyploid ancestry, we generally assume maternal inheritance of the chloroplast genome, although biparental inheritance has been noted in some cactus species (Corriveau and Coleman 1988, Zhang et al. 2003). Here we present a denser sampling of both diploid and polyploid species than other recent studies of the Cylindropuntieae, with the goal of bringing new insights into the natural history of the chollas.

Materials and Methods

Taxon Sampling

All sequences analyzed in the present study were generated from specimens we collected in the field or obtained from the Desert Botanical Garden (Phoenix, AZ). We aimed for exhaustive sampling of the species, regardless of ploidy, with multiple representatives included in the analysis where sample supply and PCR success allowed. *Opuntia littoralis* (Engelm.) Cockerell served to root the trees. A total of 86 exemplars representing 51 species were analyzed; taxon authorship and reported chromosome numbers are provided in Table 1.

DNA Extraction and Analysis

DNA extraction was performed on lyophilized stem tissue following the protocol of Pepper and Norwood (2001). DNA amplification primer sequences for the *trnH*$^{(GUG)}$*-psbA* intergenic spacer, the *rpL16* intron, and the *rpS16* intron followed Shaw et al. (2005), and for the *trnQ*$^{(UUG)}$*-5′rpS16* intergenic spacer, Shaw et al. (2007). Amplification of all regions used the following parameters: 80°C, 5 min; 35X (95°C, 1 min; 50°C, 1 min with a ramp of 0.3°C/s; 65°C, 4 min); 65°C, 5 min. Sequencing of purified PCR products (PureLink kit: Invitrogen, San Diego, CA) utilized the same primers as PCR, and was carried out by Retrogen, Inc. (San Diego, CA). Alignment of resulting sequences (Genbank accession numbers: Table 1) was done using MUSCLE (service of EMBL-EBL: ebi.ac.uk/Tools/msa/muscle/) and by eye; gaps were treated as missing data. Except for the Bayesian and parsimony analyses, indels were added to the data set as binary characters following a simple indel coding strategy (Simmons and Ochoterena 2000). Highly variable microsatellite loci (combinations of mostly uni-, di-, and trinucleotide repeats) were excluded from the analyses.

Phylogenetic analyses using maximum likelihood (ML) and Bayesian inference (BI) were performed on the CIPRES Science Gateway (Miller et al. 2010). ML analysis (RAxML 8.2.12 on XSEDE, Stamatakis 2014) employed the GTRGAMMA model of nucleotide substitution to estimate the best tree and calculate bootstrap support for the branches. Automated model selection in PAUP* (version 4.0a build 162, Sinauer Associates, Sunderland, MA) identified sequence evolution model HKY + I + G, which was employed for the BI analysis (MrBayes 3.2.6 on XSEDE, Ronquist et al. 2012). Four Markov Chain Monte Carlo (MCMC) chains were run for 1,500,000 generations, with sampling every 100 generations. Assessment of stationarity of -*ln*L values of these trees informed a 20% burn-in, and the remaining trees were used to construct a majority-rule consensus tree. Parsimony bootstrap values were generated using the PAUP* "fast" option and 100,000 replicates.

Results

We generated all 339 sequences analyzed in the present study (Table 1); five sequences are missing due to amplification or sequencing failure. The aligned and concatenated sequence data set totaled 3147 bases (*trnH*$^{(GUG)}$*-psbA* =481; *rpL16* =1188; *rpS16* =858; *trnQ*$^{(UUG)}$*-5′rps16* =620), of which 162 were excluded due to sequence ambiguity or the hypervariability associated with microsatellite loci; the sequences of this refined set yielded 24, 81, 34, and 27 parsimony informative characters, respectively. Thirty binary characters were added to the analysis to account for indel variation, for use in the Bayesian and parsimony bootstrap analyses.

There was no conflict among the Maximum Likelihood Best Tree (= ML best tree), the Bayesian Consensus Tree, and the Parsimony Bootstrap Tree, allowing us to use the ML Best Tree to show topology, branch length, and clade support from all analyses (Fig. 1). At the base of all trees, a poorly supported (60% Maximum Likelihood Bootstrap–MB, 52% Bayesian Posterior Probability–BP, 56% Parsimony bootstrap–PB) clade bears *Micropuntia pulchella* (Engelm.) M.P.Griff. and *Pereskiopsis* and is sister to the strongly supported (100%, 100%, 98%) clade of *Cylindropuntia* and remaining *Grusonia* (including *Corynopuntia* and *Marenopuntia)* species (Fig. 1). This echoes previous studies (Barcenas 2016; Griffith and Porter 2009; Majure et al. 2019) that showed substantial distinction of *Micropuntia pulchella* from any other species of *Grusonia*.

All trees exhibit the *Grusonia* + *Cylindropuntia* trichotomy, which is supported by eight synapomorphies, including a large deletion. Although this creates uncertainty about the monophyly of *Cylindropuntia* (Fig. 1), these same clades were resolved by Barcenas (2016) and Majure et al. (2019), but with *Grusonia* sister to a monophyletic *Cylindropuntia*, supported by 79% MB, 57% BP, and 100% PB (Barcenas 2016), and by 100% MB and PB (Majure et al. 2019). The three clades are labeled Cylindropuntia I, Cylindropuntia II, and Grusonia and are supported by three, eleven, and six apomorphies, respectively, with high support from each measure (Fig. 1). Thirty indels were coded and used only in the Bayesian analysis, and included 0, 5, and 1

TABLE 1. NOMENCLATURAL GUIDE TO THE SPECIMENS INCLUDED FOR DNA SEQUENCE ANALYSIS. Chromosome counts (in brackets; obtained from Pinkava 2002, Baker and Pinkava 2018) refer to the taxon, not these samples. Collection and voucher information: Desert Botanical Garden (DES), San Diego Natural History Museum (SD), Sul Ross University (SRSC); the remaining collections display collection and accession numbers referring to living specimens at the Desert Botanical Garden or the San Diego Botanic Garden (marked SBG). Genbank accession numbers are provided separately for the chloroplast introns and spacers examined: *rp*L16, *rp*S16, *trn*H, and *trn*Q; dashes note missing sequences. An asterisk (*) indicates collection information only.

Taxon	Terminal (Fig. 1)	Collection	*rp*L16	*rp*S16	*trn*H	*trn*Q
***Cylindropuntia* (Engelm.) F.M.Knuth**						
C. abyssi (Hester) Backeb. [22]	abyssii26505	Hodgson 26505 2020-0313-01	MW419436	MW419520	MW419604	MW419690
	abyssi2652	Hodgson 26520 2020-0314-01	MW419437	MW419521	MW419605	MW419691
C. acanthocarpa (Engelm. & Bigelow) F.M.Knuth [22] var. *acanthocarpa*	acanthocarpa0238	Hodgson 8115 1994-0238-0101	MW419438	MW419522	MW419606	MW419692
	acanthocarpa569	Baker 7878 1990-0569-0101	MW419439	MW419523	MW419607	MW419693
	acanthocarpa170	Quirk s.n. 1985-0170-0102	MW419440	MW419524	MW419608	MW419694
C. alcahes (F.A.C.Weber) F.M.Knuth [22, 33] var. *alcahes*	alcahes0064	Trelease s.n. 2009-0064-0101	MW419441	MW419525	MW419609	MW419695
	alcahes4835	SD: Rebman 4835	MW419442	MW419526	MW419610	MW419696
var. *burrageana* (Britton & Rose) Rebman	alcahesburr024	Baker s.n. 2010-0024-0101	MW419443	MW419527	MW419611	MW419697
	alcahesburr671	Rebman 2865 1994-0671-1001	MW419444	MW419528	MW419612	MW419698
C. anteojoensis (Pinkava) E.F. Anderson [44]	anteojoensis0089	Lott s.n. 1976-0089-0101	MW419445	MW419529	MW419613	MW419699
C. arbuscula (Engelm.) F.M. Knuth [66]	arbuscula201	Baker s.n. 1995-0201-0101	MW419446	MW419530	MW419614	MW419700
C. bernardina (Engelm. ex Parish) M.A. Baker et al.) [22]	bernardina624	SD: Mayer 624	MW419447	MW419531	MW419615	MW419701
C. bigelovii (Engelm.) F.M. Knuth [22, 33] var. *bigelovii*	bigelovii620	SD: Mayer 620	MW419448	MW419532	MW419616	MW419702
	bigelovii4956	SD: Rebman 4956	MW419449	MW419533	MW419617	MW419703
var. *ciribe* (Engelm. Ex J.M.Coult.) Rebman [22]	bigeloviiciribe5173	SD: Rebman 5173	MW419450	MW419534	MW419618	MW419704
C. californica (Torrey & A.Gray) F.M.Knuth [22] var. *californica*	californica575	Baker s.n. 1993-0575-0101	MW419451	MW419535	MW419619	MW419705
var. *rosarica* (G.E.Linds.)Rebman	californicaros917	unknown 1987-0917-0101	MW419452	MW419536	MW419620	MW419706
C. calmalliana (J.M.Coulter) F.M.Knuth [66]	calmalliana599	Baker s.n. 1993-0599-0101	MW419453	MW419537	MW419621	MW419707
	calmalliana673	Rebman 2822 1994-0673-1001	MW419454	MW419538	MW419622	MW419708

TABLE 1. CONTINUED

Taxon	Terminal (Fig. 1)	Collection	*rp*L16	*rp*S16	*trn*H	*trn*Q
C. caribaea (Britton & Rose) F.M.Knuth [?]	caribaea0356	Huntington Gardens s.n. 2004-0356-0109	MW419455	MW419539	MW419623	MW419709
C. cedrosensis Rebman [?]	cedrosensis2495	SD: Rebman 2495	———	———	MW419624	MW419710
C. cholla (F.A.C.Weber) F.M.Knuth [22, 33, 44]	cholla189	Thompson Arboretum s.n. 1939-0189-0101	MW419456	MW419540	MW419625	MW419711
	cholla4501	SD: Rebman 4501	MW419457	MW419541	MW419626	MW419712
C. delgadilloana J.Rebman & D.Pinkava [22]	delgadilloana712	Rebman 2560 1994-0712-1002	MW419458	MW419542	MW419627	MW419713
C. echinocarpa (Engelm. & Bigelow) F.M.Knuth [22]	echinocarpa626	SD: Mayer 626	MW419459	MW419543	MW419628	MW419714
	echinocarpa7728	Baker 7728 1990-0564-01	MW419460	MW419544	MW419629	MW419715
C. fosbergii C.B.Wolf [33]	fosbergii606	SD: Mayer 606	MW419461	MW419545	MW419630	MW419716
C. fulgida (Engelm.) F.M.Knuth [22, 33]	fulgida342	Hodgson 17454 2003-0342-0101	MW419462	MW419546	MW419631	MW419717
	fulgida568	Baker 7880 1990-0568-0101	MW419463	MW419547	MW419632	MW419718
	fulgida5281	SD: Rebman 5281	MW419464	MW419548	MW419633	MW419719
C. gander (C.B.Wolf) Rebman & Pinkava [22] subsp. *ganderi*	ganderi4077	SD: Rebman 4077	MW419465	MW419549	MW419634	MW419720
	ganderi4957	SD: Rebman 4957	MW419466	MW419550	MW419635	MW419721
subsp. *catavinensis* (Rebman) Rebman	gandericata166	Baker s.n. 2011-0166-0101	MW419467	MW419551	MW419636	MW419722
C. imbricata (Haw.) F.M.Knuth [22]	imbricata0048	Puente 4103 2009-0048-0103	MW419468	MW419552	MW419637	MW419723
	imbricata0059	Ward 363 2008-0059-0101	MW419469	MW419553	MW419638	MW419724
C. kleiniae (DC.) F.M.Knuth [44]	kleiniae0886	Leon s.n. 1993-0886-1001	MW419470	MW419554	MW419639	MW419725
C. leptocaulis (DC.) F.M.Knuth [22, 33, 44]	leptocaulis190	Kaumen s.n. 1978-0190-0201	MW419471	MW419555	MW419640	MW419726
	leptocaulis196	Kaumen s.n. 1978-0196-0201	MW419472	MW419556	MW419641	MW419727
C. lindsayi (Rebman) Rebman [44]	lindsayi127	Ward s.n. 2011-0127-0101	MW419473	MW419557	MW419642	MW419728
	lindsayi165	Baker s.n. 2011-0165-0101	MW419474	MW419558	MW419643	MW419729
C. molesta (Brandegee) F.M.Knuth [88]	molesta0244	Pinkava 8786 1973-0244-0102	MW419475	MW419559	MW419644	MW419730
C. munzii (C.B.Wolf) Backeb. [22, 33]	munzii4970	SD: Rebman 4970	MW419476	MW419560	MW419645	MW419731
C. prolifera (Engelm.) F.M.Knuth [22, 33, 66]	prolifera638	SD: Mayer 638	MW419477	MW419561	MW419646	MW419732
	prolifera3951	SD: Rebman 3951	MW419478	MW419562	MW419647	MW419733
C. ramosissima (Engelm.) F.M.Knuth [22, 33]	ramosissima28	Ward s.n. 2007-0028-0101	MW419479	MW419563	MW419648	MW419734

TABLE 1. CONTINUED

Taxon	Terminal (Fig. 1)	Collection	*rp*L16	*rp*S16	*trn*H	*trn*Q
	ramosissima909	Gass s.n. 1985-0909-2101	MW419480	MW419564	MW419649	MW419735
C. sanfelipensis (Rebman) Rebman [66]	sanfelipensis42	Rebman s.n. 1999-0042-0101	MW419481	MW419565	MW419650	MW419736
C. santamaria (E.M.Baxter) Rebman [22]	santamaria2785	SD: Rebman 2785	MW419482	———	MW419651	MW419737
C. spinosior (Engelm.) F.M.Knuth (= C. imbricata subsp. spinosior, Baker et al. 2019) [22]	spinosior0178	unknown 2003-0178-0101	MW419483	MW419566	MW419652	MW419738
C. tesajo (Engelm. ex Coult.) F.M.Knuth [22]	tesajo35	Lindsay s.n. 1939-0035-0102	MW419484	MW419567	MW419653	MW419739
	tesajo53	Rebman 4972 1999-0053-0101	MW419485	MW419568	MW419654	MW419740
C. tunicata (Lehmann) F.M.Knuth [22, 33]	tunicata345	Puente s.n. 2004-0345-0101	MW419486	MW419569	MW419689	MW419741
	tunicata568	Baker 6255 1985-0568-0108	MW419487	MW419570	MW419655	MW419742
C. versicolor (Engelm. ex Coult.) F.M.Knuth (= *C. thurberi* subsp. *versicolor* , Baker et al. 2019) [22]	versicolor0035	Hodgson 16449b 2003-0035-0103	MW419488	MW419571	MW419656	MW419743
C. whipplei (Engelm. & Bigelow) F.M.Knuth [22, 44]	whipplei0001	Hodgson s.n. 2007-0001-0101	MW419489	MW419572	MW419657	MW419744
	whipplei25441	DES: Hodgson 25441	MW419490	MW419573	MW419658	MW419745
C. wolfii (L.D.Benson) M.A.Baker [66]	wolfii594	SD: Mayer 594	MW419491	MW419574	MW419659	MW419746
	wolfii3820	SD: Rebman 3820	MW419492	MW419575	MW419660	MW419747
***Grusonia* Rchb.f. ex Britton & Rose**						
G. aggeria (Ralston & Hilsenb.) E.F.Anderson [22]	aggeria2314	SRSC: Fenstermacher 2314	MW419493	MW419576	MW419661	MW419748
	aggeria3495	Marshall s.n. 1952-3495-01-1	MW419494	MW419577	MW419662	MW419749
G. bradtiana (J.M.Coult.) Britton & Rose [22]	bradtiana141	Evans s.n. 1978-0141-01-3	MW419495	MW419578	MW419663	MW419750
	bradtiana5660	Mieg 42 1956-5660-0101	MW419496	MW419579	MW419664	MW419751
G. bulbispina (Engelm.) H.Robinson [44]	bulbispina804	Dodson et al. s.n. 1990-0804-02-2	MW419497	MW419580	MW419665	MW419752
G. clavata (Engelm.) H.Robinson [22]	clavata6404	Russell s.n. 1959-6404-01-1	MW419498	MW419581	MW419666	MW419753
G. densispina (Ralston & Hilsenb.) Pinkava [44]	densispina0124	Zimmerman 2859 2010-0124-01-2	MW419499	MW419582	MW419667	MW419754
	densispina2306	DES*: Fenstermacher 2306	MW419500	MW419583	MW419668	MW419755
G. emoryi (Engelm.) Pinkava [44]	emoryi0112	Felger 88-11 1988-0112-02-1	MW419501	MW419584	MW419669	MW419756
	emoryi10897	Baker 10897 1995-0204-01	MW419502	MW419585	MW419670	MW419757
G. grahamii (Engelm.) H.Robinson [44]	grahamii0705	Zimmerman 2546A 1988-0705-02-1	MW419503	MW419586	MW419671	MW419758

TABLE 1. CONTINUED

Taxon	Terminal (Fig. 1)	Collection	*rp*L16	*rp*S16	*trn*H	*trn*Q
	grahamii1142	SRSC: Fenstermacher 1142a	MW419504	MW419587	MW419672	MW419759
	grahamii2442	DES*: Fenstermacher 2442	MW419505	MW419588	MW419673	MW419760
G. invicta (Brandegee) E.F.Anderson [22]	invicta0033	Tegelberg s.n. 1939-0033-01-1	MW419506	MW419589	MW419674	MW419761
	invicta75	Voss s.n. 75.0060P (SBG)	MW419507	MW419590	MW419675	MW419762
G. marenae (S.H.Parsons) E.F.Anderson [?]	marenae7265	McGill s.n. 1962-7265-01-2	MW419508	MW419591	MW419676	MW419763
	marenae8491	Gentry s.n. 1966-8491-01-1	MW419509	MW419592	MW419677	MW419764
G. moelleri (A. Berger) E.F.Anderson [22]	moelleri9412	Quirk s.n. 1968-9412-02-6		MW419593	MW419678	MW419765
G. parishii (Orcutt) Pinkava [22]	parishii027	Wolf 8296 2007-0027-01	MW419510	MW419594	MW419679	MW419766
	parishii0565	Baker 7550.1 1990-0565-01-1	MW419511	MW419595	MW419680	MW419767
G. schottii (Engelm.) Robinson [66]	schottiiJFSN	DES*: Fenstermacher s.n.	MW419512	MW419596	MW419681	MW419768
G. vilis (Rose) H. Robinson [?]	vilis12834	Baker 12834 2019-0031-01	MW419513	MW419597	MW419682	MW419769
G. wrightiana (E.M.Baxter) E.M.Baxter [44]	wrightiana17601	Baker 17601.1 2019-0351-01	MW419514	MW419598	MW419683	MW419770
***Micropuntia* Daston**						
Micropuntia pulchella (Engelm.) M.P.Griff. [22]	pulchella17770	DES*: Baker 17770.1	MW419515	MW419599	MW419684	———
	pulchella17776	DES*: Baker 17776.3	MW419516	MW419600	MW419685	MW419771
Opuntia littoralis (Engelm.) Cockerell	Opuntialittoralis	SD: Mayer 639	MW419517	MW419601	MW419686	MW419772
Pereskiopsis porteri (Brandegee) Britton & Rose	porterii109	DBG s.n. 1975-0109-21-1	MW419518	MW419602	MW419687	MW419773
	porteri537	Quirk s.n. 1984-0537-01-2	MW419519	MW419603	MW419688	MW419774

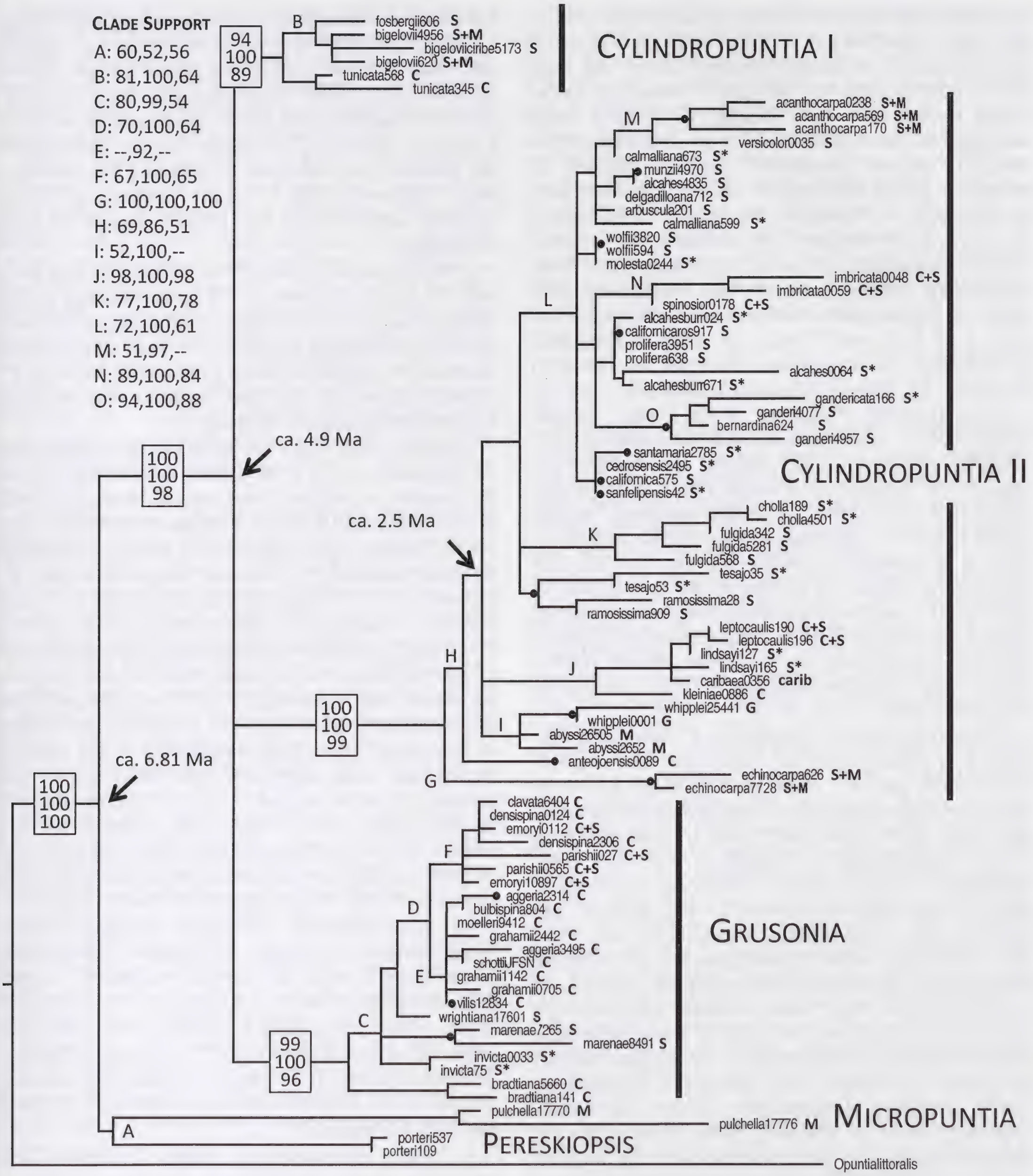

FIG. 1. Best tree resulting from Maximum Likelihood analysis of cpDNA sequence data, presented as a phylogram. Support noted for clades include Maximum Likelihood Bootstrap percentage, Bayesian Posterior Probability, and Parsimony Bootstrap percentage, respectively. Black dots mark clades or species exhibiting dry fruit; after the specimen identifier, C, M, and S refer to species range in Chihuahuan, Mohave, or Sonoran deserts, respectively. The arrows connect the estimated origin date (Hernandez-Hernandez et al. 2014) to selected nodes.

synapomorphies, respectively, for the aforementioned clades.

On the Grusonia clade, *G. bradtiana* (J.M.Coult.) Britton & Rose, the type species of *Grusonia* and native of the Chihuahuan desert (Mexican state of Coahuila), is shown as sister to the rest of the Grusonia clade, which corresponds to *Corynopuntia* F.M.Knuth (Fig. 1). The trichotomy at the base of this clade features the lineages of *G. invicta* (Brandegee) E.F.Anderson (central Baja California, Mexico) and *G. marenae* (S.H.Parsons) E.F.Anderson (Sonora, Mexico), the latter species having formerly

been described as a monotypic genus (*Marenopuntia marenae* Backeberg). *Grusonia wrightiana* (E.M.Baxter) E.M.Baxter (Sonoran desert and Baja California) is sister to the larger remaining clade, which is split into two lineages (Fig. 1): a more southern-centered clade of U.S. and Mexican Chihuahuan desert species (*G. aggeria* (Ralson & Hilsenb.) E.F.Anderson, *G. bulbispina* (Engelm.) H.Robinson, *G. grahamii* (Engelm.) H.Robinson, *G. moelleri* (A.Berger) E.F.Anderson, *G. schottii* (Engelm.) Robinson, and *G. vilis* (Rose) H. Robinson) and a more northern- and western-centered clade of Chihuahuan, Sonoran and Mohave desert species of U.S. and Mexico (*G. clavata* (Engelm.) H.Robinson, *G. densispina* (Ralston & Hilsenb.) Pinkava, *G. emoryi* (Engelm.) Pinkava, and *G. parishii* (Orcutt) Pinkava). Both clades include species of a group called the *Grusonia schottii* complex (*G. aggeria, G. emoryi, G. grahamii, G. schottii, G. densispina*; Ralston 1987; Ralston and Hilsenbeck 1989, 1992), revealing paraphyly of this group unless it is expanded to also include at least *G. clavata, G. parishii, G. bulbispina*, and *G. vilis*. The two representatives of *G. emoryi* do not appear as sisters in this northwestern clade, which may indicate divergence that warrants reconsideration of *G. stanlyi* Engelm. (represented by specimen Baker 10897), which had been synonymized with *G. emoryi* by Pinkava (1999).

Cylindropuntia I, comprising *C. bigelovii* (Engelm.) F.M.Knuth, *C. tunicata* (Lehmann) F.M.Knuth, and *C. fosbergii* C.B.Wolf, combines species of series *Bigelovianae* and *Imbricatae* (Britton and Rose 1919; Hunt 2006), and is thus surprising from a morphological perspective. The close relationship of *Cylindropuntia bigelovii*, a common species from Baja California to the Mojave and Sonoran desert of Mexico, CA, AZ, NV, and NM., and *C. tunicata*, which is widespread in the Chihuahuan desert of central and northern Mexico to southern Texas, has been revealed only recently (Barcenas 2016; Majure et al. 2019). But despite their differences, both species produce stem segments that are easily detached, have prominent tubercules, similar numbers of spines per areole, and similar size and colors of glochids. Both produce fleshy, spineless fruits, and both species have the unusual distinction of producing roots of medicinal value to indigenous people, *C. bigelovii* as a laxative and *C. tunicata* as a diuretic (Anderson 2001).

Cylindropuntia II bears the majority of *Cylindropuntia* species, and features a basal branch that bears *C. echinocarpa* (Engelm. & Bigelow) F.M.Knuth, which is widespread in the Mohave and Sonoran deserts of Baja California and Sonora, as well as in California, Nevada, and Arizona.

Cylindropuntia anteojoensis (Pinkava) E.F.Anderson is sister to the remainder of this clade; trees with lower support (not shown) commonly placed this species on a clade with *C. ramosissima* (Engelm.) F.M.Knuth and *C. tesajo* (Engelm. ex Coult) F.M.Knuth, which form a more derived clade (Fig. 1)—a pattern also shown by Barcenas et al. (2016) and Majure et al. (2019). All three species exhibit narrow "pencil-like" stems and dry fruit; *C. anteojoensis* is eastern-most, in the Chihuahuan desert of Coahuila, Mexico; *C. ramosissima* is widespread in the Sonoran and Mohave deserts and northeastern Baja California, and *C. tesajo* appears to be an endemic derivative of the former species in Baja California.

Cylindropuntia cholla (F.A.C.Weber) F.M.Knuth and *C. fulgida* (Engelm.) F.M.Knuth form a clade; both species produce fleshy, proliferating fruits, and are similar in stature and flower color. *Cylindropuntia cholla* is a species of Baja California, whereas *C. fulgida* ranges from Arizona south into the states of Sonora and Sinaloa in Mexico.

Another clade bears the widespread *Cylindropuntia leptocaulis* (DC.) F.M.Knuth, whose range spans the breadth of northern and central Mexico, as well as the southern U.S., from Arizona to Oklahoma and Texas. Sharing this clade are *C. lindsayi* (Rebman) Rebman, endemic to southern Baja California, *C. kleiniae*, of the Chihuahuan desert of the U.S. and Mexico, and *C. caribaea* (Britton & Rose) F.M.Knuth, the sole cholla of the Caribbean, native to Hispaniola. It is not clear whether dispersal or vicariance are responsible for the isolation and speciation of *C. lindsayi* and *C. caribaea*. The species of this clade share tall stature (1.8–3 m) slender (pencil-like) stem segments, and fleshy fruit. The presence of the tetraploid *C. kleiniae* and *C. lindsayi* on this clade with *C. leptocaulis*, which exists in diploid, triploid, and tetraploid forms, suggests one or more of these species could be an allopolyploid, and at least one of the others could be a parent.

The more northern and upland species *Cylindropuntia whipplei* (Engelm. & Bigelow) F.M.Knuth shares a clade with the narrow endemic *C. abyssi* (Hester) Backeb., which is suspected to be of hybrid origin, possibly involving *C. bigelovii* or *C. acanthocarpa* (Engelm. & Bigelow) F.M.Knuth (Pinkava 2003; Hunt 2006). If *C. abyssi* is indeed a hybrid, the present study provides evidence that the maternal parent is *C. whipplei*.

A large, well-supported lineage comprises the remaining species of this clade. Although morphologically diverse, these species share a distribution that is limited to the more western and northern deserts (Sonoran, Mohave, and Baja California). Much of the structure revealed in the analysis of this clade is not robust, but some patterns merit consideration.

Cylindropuntia acanthocarpa and *C. versicolor* (Engelm. ex Coult.) F.M.Knuth overlap in range in the Sonoran Desert of Arizona and Mexico. Note that recent work has reduced *C. versicolor* to a subspecies of *C. thurberi* (Engelm.) F.M.Knuth (Baker et al. 2019), which could not be represented in the present study.

Besides sharing a clade, *Cylindropuntia imbricata* (Haw.) F.M.Knuth and *C. spinosior* (Engelm.) F.M.Knuth also have overlapping ranges in the deserts of Arizona, New Mexico, and northern Mexico. Baker et al. (2019) have also reduced *C. spinosior* to a subspecies of *C. imbricata*.

Three narrow endemics of Baja California: *C. cedrosensis* Rebman (Isla de Cedros), *C. santamaria* (E.M.Baxter) Rebman (Isla Magdalena), and *C. sanfelipensis* (Rebman) Rebman (San Felipe Desert), share a clade with the more widespread *C. californica* var. *californica* (Torrey & A.Gray) F.M.Knuth, suggesting a possible progenitor role for the latter species. Due to its similarity to *C. wolfii* (L.D.Benson) M.A.Baker, we expected that *C. sanfelipensis* would show a close relationship with that species. However, the hexaploid genome of *C. sanfelipensis* may indicate an allopolyploid origin that might have included paternal contributions from *C. wolfii*, also a hexaploid.

Cylindropuntia ganderi (C.B.Wolf) Rebman & Pinkava) has been segregated from *C. acanthocarpa* (Rebman 2001), a change that is entirely justified by the distinction these taxa exhibit in the tree. The position of *C. bernardina* (Engelm. ex Parish) M.A.Baker et al., formerly *C. californica* var. *parkeri* (J.M.Coult.) Pinkava, as a sister to specimens of *C. ganderi,* rather than the other varieties of *C. californica,* affirms its recent recognition (Baker and Pinkava 2018). *Cylindropuntia bernardina* is found at the northern edge of the range of *C. ganderi* in southern California.

The presence of *C. alcahes* (F.A.C.Weber) F.M.Knuth and *C. prolifera* (Engelm.) F.M.Knuth together on a clade is expected, as the latter probably originated via hybridization of the former with *C. cholla* (Mayer et al. 2000). The placement of a representative of *C. californica* var. *rosarica* (G.E.Linds.) Rebman on this clade, isolated from *C. californica* var. *californica,* is another indicator that this taxon needs additional study.

The union of *C. molesta* (Brandegee) F.M.Knuth and *C. wolfii* on a clade is unexpected and may be spurious. Alternatively, the hexaploid *C. wolfii* and the octoploid *C. molesta* may share genomes through allopolyploid ancestry.

Discussion

Our work concurs with previous studies that propose reviving *Micropuntia* to recognize a monotypic *M. pulchella* (Griffith 2002; Griffith and Porter 2009; Barcenas 2016; Majure et al. 2019). *Grusonia* (*Micropuntia*) *pulchella* does not share a clade with the other members of the Grusonia clade, which in fact share a more recent ancestor with *Cylindropuntia*. The morphological and ecological case for *Micropuntia pulchella* is also strong, including unique features of the stem tuber, spine angle, areole wool, habit, and geography (Griffith 2002).

The topology of the Grusonia clade supports either a monotypic *Grusonia* (= *G. bradtiana* Britton and Rose) and monophyletic *Corynopuntia* F.M.Knuth, or a *Grusonia sensu lato* (Stuppy 2002), which includes the entire clade. The former taxonomic proposal, however, seems to overemphasize the distinction of *G. bradtiana* from the remaining species of the Grusonia clade, either morphologically or genetically (Fig. 1; see Majure et al. (2019) for a thorough examination of the options for *Grusonia* taxonomy). Consequently, we concur with those (Robinson 1973; Majure et al. 2019) promoting subsuming all *Corynopuntia* species into a more inclusive *Grusonia*.

History of the Chollas

Ancestral elements of subfamily Opuntioideae originated in the central Andes of South America, and with other lineages of Cactaceae extended their range into North America (Raven and Axelrod 1978; Wallace and Dickie 2002). The northward migration and radiation of the chollas appears tied to the expansion of the North American deserts beginning in the mid-Miocene (Arakaki et al. 2011; Hernandez-Hernandez et al. 2014), approximately 8-15 mya (Van Devender and Brusca 2015). The emergence of tribe Cylindropuntieae has been estimated to be 9.05 mya (no credibility interval provided; Hernandez-Hernandez et al. 2014), although a more recent estimate places the origin at approximately 17.9 mya (14.8-20.4 mya; Majure et al. 2019). Cylindropuntieae probably originated in South America and expanded north, evidenced by the South American endemic *Quiabentia*: opuntioids with large, persistent leaves and other plesiomorphic features. *Pereksiopsis*, the other leafy, non-cholla genus of the tribe is native to southern Mexico; therefore the "cholla" elements of tribe Cylindropuntieae are products of the North American deserts, ranging from central Mexico to the southern and western United States.

Divergence time analyses of Hernandez-Hernandez et al. (2014) calculated a date of 4.9 mya (ca. 2.7-7.7 mya) for the common ancestor of *Grusonia* + *Cylindropuntia*. This suggests a late Miocene-Pliocene time frame for divergence of the three major clades of chollas; an earlier date of 12 mya (9.3-14.5 mya) has also been suggested (Majure et al. 2019). However, both sets of estimates suggest a great deal of cholla speciation occurred during the Pleistocene, <2.5 mya.

The Hernandez-Hernandez et al. (2014) study of 224 species, representing ca. 85% of the generic diversity of the Cactaceae, also detected a significantly heightened diversification rate for the *Grusonia* + *Cylindropuntia* clade—which is most evident in the branch lengths of clade Cylindropuntia II (Fig. 1). Studies of diversification times in *Cereus* (Silva et al. 2017) and *Pilosocereus* (Lavor et al. 2019) support the hypothesis that the multiple glacial and interglacial episodes of the Pleistocene drove the radiation of

TABLE 2. COMPARISON OF CHROMOSOME NUMBER, RANGE SIZE, AND SISTER SPECIES STATUS FOR SELECTED PAIRS OF *CYLINDROPUNTIA* SISTER SPECIES.

Sister species	Chromosome number	Range (W=widespread, N=narrow)	Isolation
C. leptocaulis	22, 33, 44	W: across northern Mexico and southern U.S.	Sea of Cortez
C. lindsayi	44	N: Baja California Sur	
C. ramosissima	22, 44	W: Mojave and Sonoran deserts of U.S. and Mexico, and extreme northeastern Baja California	Sea of Cortez
C. tesajo	22	N: Central Baja California	
C. whipplei	22, 44	W: high desert, grassland, sagebrush, and pine forest of AZ, CO, NM, and UT, U.S.	Peripatric?
C. abyssi	22	N: Mohave Co., AZ, U.S.	
C. bigelovii	22, 33	W: Sonoran desert of U.S. and Baja California	Peripatric?
C. fosbergii	33	N: one population in eastern San Diego Co., CA	
C. cholla	22, 33, 44	W: throughout Baja California	Sea of Cortez
C. fulgida	22, 33	W: Sonoran desert of U.S. and northern Mexico	

these genera. Expansion and contraction of the North American deserts occurred repeatedly through the Pleistocene, with the most recent expansion of the Sonoran desert into southern Arizona and California occurring just 9000 years ago (Van Devender and Brusca 2015). The formation of the Gulf of California (Sea of Cortez) may have had a role in the divergence of at least three sister-species pairs: *C. cholla*/*C. fulgida, C. leptocaulis*/*C. lindsayi*, and *C. ramosissima*/*C. tesajo* (Table 2); the Gulf started opening approximately 10 mya and is still widening (Moore and Buffington 1968).

The increase in diversification rate noted in the chollas may have been facilitated not only by desertification and climate fluctuation, but also by intrinsic genetic and reproductive processes of these taxa. Hybridization is common among chollas, and can lead to the origin of fertile allopolyploid species, but autopolyploidy is also common (Pinkava 2002). Moreover, the ability of chollas to reproduce vegetatively via stem segment propagules can allow sterile odd-ploidy auto- and allopolyploids to not only survive, but possibly benefit from the dosage effects of extra sets of chromosomes (Baker and Pinkava 1987, 2018; Pinkava 2002). Six *Cylindropuntia* species (*C. alcahes, C. bigelovii, C. fulgida, C. munzii* (C.B.Wolf) Backeb., *C. ramosissima*, and *C. tunicata*) exist as diploids or triploids, and in at least one species, *C. bigelovii*, the triploids exhibit a greater number of plants and size of range than the diploids (Pinkava 2002). In general, polyploidy in subfamily Opuntiodeae has been detected in 64.3% of species, a rate that far exceeds the other subfamilies (Cactoideae = 12.5%, Pereskioideae = 0.0%) (Pinkava 2002). Our calculation of polyploidy rates, omitting hybrids, is 60% for *Cylindopuntia* and 47% for *Grusonia* (see Baker and Pinkava 2018). Moreover, in twelve of forty C*ylindropuntia* species, autopolyploidy has resulted in at least two ploidal levels, in *Grusonia* it is eight of 17 species (Table 1). And among the clades bearing *Cylindropuntia* species (Fig. 1), in every case where there are clear sister-species pairs that differ in numbers of documented ploidy levels, the species with greater ploidal variation have larger ranges, usually much larger (Table 2). This pattern may simply indicate a correlation between population size and potential for ploidy variation, or it may indicate the potential niche diversity that accompanies ploidal level diversity, a consequence of the myriad ways polyploidy stokes the evolutionary potential of plants (Stebbins 1950; Soltis and Soltis 2000; Baker and Pinkava 2018).

Cylindropuntia I and II. A monophyletic *Cylindropuntia* did not achieve sufficient support in our analyses, although this resolution has been found in other studies (Barcenas 2016; Majure et al., 2019). The cholla trichotomy suggests a rapid divergence of these three clades during the formation of the deserts of North America. Subsequent to this divergence, however, there are differences in the stem and crown branch lengths of these three clades, with the starkest contrast shown between Cylindropuntia I and Cylindropuntia II (Fig. 1). Cylindropuntia II exemplifies the diversification rate increase (Hernandez-Hernandez et al. 2014) discussed above, but could the absence of a similar level of diversification and divergence in Cylindropuntia I to some degree reflect mode of reproduction? Excluding the triploid specimens (Table 1), normal levels of fertility are reported for the species of Cylindropuntia II, except *C. cholla*, *C. fulgida*, and *C. molesta*. In contrast, the taxa of Cylindropuntia I, *C. tunicata*, *C. bigelovii*, and *C. fosbergii*, show an almost complete reliance on asexual reproduction. The range of *C. bigelovii* var. *bigelovii* consists mostly of sterile triploid populations, with just a few known diploid populations; interestingly, the narrow Baja California endemic, *C. bigelovii* var. *ciribe* is diploid and fertile (Rebman 2001; Pinkava 2002). *Cylindropuntia fosbergii* exists only as sterile triploids in a single diffuse population in southern California (Mayer et al. 2011; Baker et al. 2012). Some consider *C. fosbergii* a hybrid between *C. bigelovii* and an unidentified species, but Mayer et al. (2011) found insufficient evidence for a hybrid

origin of *C. fosbergii* and hypothesize a sister relationship for it and *C. bigelovii*. *Cylindropuntia tunicata* exists in diploid and triploid forms, but the fruits of diploids are mostly sterile (Anderson 2001). *Cylindropuntia rosea* (DC.) Backeb., not sampled in this study, is the only other species of this clade and while its fertility in its native range (states of Hidalgo and Puebla, Mexico) is unclear, it reportedly produces inviable seeds in introduced populations in Australia (Hosking et al. 2007).

Asexual reproduction is a key reproductive and survival strategy in chollas (Pinkava 2002), and asexual lineages in general may possess a theoretical advantage over sexual lineages in diversification rate (Barraclough et al. 2003; Fontaneto et al. 2012). But under the rapidly changing selective pressures of the Pliocene through the Pleistocene, sexuality may have proven the superior mechanism for divergence and speciation of the chollas. Comparisons of genetic variation within and among populations of sexual and asexual cholla species would provide valuable insight into the genetics of adaptation and divergence.

Evolutionary Trends in the Chollas

Among *Grusonia* species, there is a general trend in plant stature and stem segment length from taller and longer, respectively, in the basal clades, to prostrate and shorter in the more derived clades. This could be construed as a response to the increasing desertification of the region. Most *Cylindropuntia* species, in contrast, exhibit an erect, shrubby to tree-like habit, but include seven species with a "pencil"-like stem segment morphology. These species, except *C. anteojoensis*, are concentrated on two different clades (*C. tesajo*/*C. ramosissima* and *C. kleiniae*/*C. caribaea*/*C. lindsayi*/*C. leptocaulis*; Fig. 1), a convergence suggesting the adaptive advantage to slender stems during the diversification of these lineages.

Adaptation to a drying climate could also account for the multiple occurrences of dry fruit production among the chollas: 3 species in Grusonia and 13 in Cylindropuntia I (Fig. 1), the latter showing at least five clades with dry fruit-fleshy fruit sister taxa. This suggests not only convergence among lineages, but a more recent (Pleistocene) shift towards a dry, burlike fruit–a clear water-saving adaptation. Additional analysis of morphological trends in Cylindropuntieae is provided in Majure et al. (2019).

Past efforts to interpret infrageneric morphological pattern among the species of *Cylindropuntia* have shown limited success. The taxonomic series proposed by Benson (1982) and Hunt (2006), identify morphological profiles that do not correlate well with the clade composition revealed in the molecular analyses presented here and elsewhere (Griffith and Porter 2009; Barcenas 2016; Majure et al. 2019, etc.). The phylogenetic patterns revealed in the present study are largely congruent with other recent studies involving chloroplast sequences (Barcenas 2016) and genomic skimming (Majure et al. 2019) in the chollas, but provoke new hypotheses of evolutionary pattern and process. Welcomed future investigations would focus on the possible synergistic adaptive value of polyploidy and vegetative propagation in the history of the chollas, and the parentage of the many hybrid diploid and polyploid taxa.

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A NEW ANNUAL SPECIES OF *CHAENACTIS* (COMPOSITAE) FROM THE CENTRAL DESERT OF BAJA CALIFORNIA, MEXICO

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ABSTRACT

A new yellow-flowered annual pincushion, *Chaenactis kyhosii* B.G.Baldwin, is described from the Central Desert of Baja California, Mexico. This desert taxon has been confused with *C. glabriuscula* DC. *sensu lato* (s. l.), a species complex of the California Floristic Province and desert periphery. *Chaenactis kyhosii* ($2n = 5_{II}$) is evidently allopatric with *C. glabriuscula* s. l. ($2n = 6_{II}$) and is distinct chromosomally. It differs morphologically from other yellow-flowered members of *Chaenactis*, including *C. glabriuscula* s. l., by the character-state combination of having non-glandular hairs sparse or lacking, main stem branches concentrated at or near base, leaves mostly basal or proximal on stems, leaf blades entire and filiform or once-pinnate with filiform lobes, peduncles and involucres densely glandular, corollas of marginal florets only slightly enlarged, cypselae sparsely white-strigose to ± glabrate, and pappi uniseriate, of four well-developed, generally unequal, and often obtuse scales. *Chaenactis kyhosii* is more closely related to the white-flowered, primarily desert-dwelling annual *C. fremontii* A.Gray, also with $2n = 5_{II}$, and the southern lineages of *C. glabriuscula* s. l. than to the northern lineages of *C. glabriuscula* s. l.

RESUMEN

Se describe un nuevo acerico anual de flores amarillas, *Chaenactis kyhosii* B.G.Baldwin, del Desierto Central de Baja California, México. Este taxón del desierto se ha confundido con *C. glabriuscula sensu lato* DC. (s. l.), un complejo de especies de la provincia florística de California y la periferia del desierto. *Chaenactis kyhosii* ($2n = 5_{II}$) es evidentemente alopátrico con *C. glabriuscula* s. l. ($2n = 6_{II}$) y es distinto por número de cromosomas. Se diferencia morfológicamente de otros miembros de *Chaenactis* de flores amarillas, incluido *C. glabriuscula* s. l., por la combinación de carácter-estados de tener pelos no glandulares encasos o ausentes, ramas del tallo principales concentradas en o cerca de la base, principalmente hojas proximales o basales, láminas foliares pinnadas con lóbulos filiformes o láminas foliares enteras y filiformes, pedúnculos e involucros densamente glandulares, corolas de las flores marginals ligeramente agrandadas, cypselae escasamente blanco-peludos a ± glabrate, y un pappus uniseriado de cuatro escamas bien desarrolladas, desiguales, a menudo obtusas. *Chaenactis kyhosii* está más estrechamente relacionado con *C. fremontii* A.Gray, un anual de flores blancas, principalmente un habitante del desierto, también con $2n = 5_{II}$, y los linajes del sur de *C. glabriuscula* s. l. que a los linajes del norte de *C. glabriuscula* s. l.

Key Words: Asteraceae, *Chaenactis kyhosii*, Chaenactideae, chromosome evolution, desert plants, dysploidy, Heliantheae alliance, Mexican flora.

Chaenactis DC. (Compositae) comprises annual, biennial, and perennial herbs and subshrubs commonly known as pincushions that occur in a wide variety of mostly open settings, from coastal bluffs to low desert and alpine environments (Morefield 2006). The genus belongs to an exclusively western North American tribe, Chaenactideae, that also includes two monotypic genera, *Dimeresia* A.Gray and *Orochaenactis* Coville (Baldwin et al. 2002). Diversity in *Chaenactis* has been interpreted variously, with recognition of as many as 49 minimum-rank taxa in 33 species (Stockwell 1940) and most recently of 24 minimum-rank taxa in 18 species (Morefield 2006). The annuals constituting *Chaenactis* sect. *Chaenactis sensu* Morefield (2006) [i.e., all annuals in the genus except *C. artemisiifolia* (Harv. & A.Gray) A.Gray, *C. carphoclinia* A.Gray, and *C. lacera* Greene, of sect. *Acarphaea*] have been challenging to taxonomists, especially *C. glabriuscula* DC. and close relatives, with differing treatments by Hall (1907), Jepson (1925), Stockwell (1940), Keck (1959), Ferris (1960), and Morefield (2006). Achieving a stable taxonomy of sect. *Chaenactis* is in part complicated by confusing patterns of morphological variation and rapid evolution of desert lineages. These desert pincushions provide valuable evidence of chromosome evolution associated with the ecological transition to arid environments, as discussed below.

Cytogenetic studies of sect. *Chaenactis* by Kyhos (1965) established that chromosomal structural rearrangements and descending dysploidization accompanied the evolution of the widespread desert-dwelling species *C. fremontii* A.Gray and *C. stevioides* Hook. & Arn., both with $2n = 5_{II}$, from ancestors in *C. glabriuscula sensu lato* (s. l.), a species complex of the Mediterranean-like California Flo-

ristic Province and desert periphery with $2n = 6_{II}$. Recent molecular phylogenetic studies have corroborated and extended Kyhos's hypothesis by showing that *C. glabriuscula* s. l. [including *C. aurea* Greene ex Rydb., *C. denudata* Nutt., *C. gracilenta* Greene, *C. heterocarpha* Torr. & A.Gray, *C. lanosa* DC., *C. orcuttiana* (Greene) Parish, *C. tanacetifolia* A.Gray, and *C. tenuifolia* Nutt.] is not monophyletic, with nested $2n = 5_{II}$ lineages corresponding to the white-flowered *C. fremontii* and *C. stevioides,* plus undescribed yellow-flowered annuals from the Desert Province of Baja California, Mexico (Baldwin and Kyhos unpublished data).

A yellow-flowered *Chaenactis* lineage with $2n = 5_{II}$ from the Central Desert of Baja California was characterized cytogenetically by Kyhos subsequent to his 1965 *Evolution* article (D. W. Kyhos, Univ. of California, Davis, personal communication). Corroborating chromosome counts were published by Turner et al. (1973), with "n = 5_{II} + 1 univalent (or fragment)" indicated on *Powell & Turner 1763* (TEX), and by Pinkava and Keil (1977), with "n = 5" indicated on *Pinkava P12163* (ASU). These annuals have been long confused with the yellow-flowered *C. glabriuscula* s. l., which occurs from northern California south into northwestern Baja California, with $2n = 6_{II}$ reported throughout its range (e.g., "5.0 km north of Colonia [Vicente] Guerrero", *Raven, Lewis & Thompson 12150* (COLO), "2n = 6_{II}"; see Raven and Kyhos 1961). Here, I describe this new species in advance of publication of the phylogenetic and other systematic findings in *Chaenactis* with D. W. Kyhos.

Taxonomic Treatment

Chaenactis kyhosii B.G.Baldwin, sp. nov. (Fig. 1). — TYPE: MEXICO, Baja California, Municipio Ensenada, Central Desert, 25.1 km S of Cataviña along Federal Highway 1, 18 May 1991, *B.G. Baldwin 764, S.J. Bainbridge, S.N. Martens* (holotype: UC; isotype: SD).

Annuals, 6–28.5 cm, sparsely arachnoid to glabrate proximally, sessile- and stipitate-glandular distally, unbranched or often 1–10 branched near base, sometimes with a well-defined central leader and 1–5 generally proximal branches. **Stems** erect to widely ascending, often reddish or stramineous. **Leaves** mostly basal and proximal cauline, entire and filiform, 1–6.5 cm long, or 1-pinnate (rarely 2-pinnate in largest plants) with blades linear to lanceolate or oblanceolate (rarely ovate) in outline, 0.5–5.5 cm long, leaf segments filiform, 1–10(–20) mm long, in 1–4(–6) loose pairs, petioles filiform, 0.35–3.5 cm long. **Capitulescences** with 1–4(–6) heads per main basal or proximal branch. **Peduncles** 2–8(–10.5) cm long, densely glandular, sometimes also sparsely and irregularly hispidulous. **Heads** discoid or ± radiant, peripheral florets only slightly enlarged, corollas ± zygomorphic or actinomorphic. **Involucres** narrowly obconic to broadly cylindric or campanulate, biseriate. **Phyllaries** 5–8 mm long, 0.7–1.4 mm wide, linear to oblance-linear, each often partially clasping the ovary of a marginal floret, green, densely glandular, sometimes also sparsely and inconspicuously arachnoid medially, apices acute to ± obtuse. **Receptacles** epaleate. **Florets** bisexual; corollas bright yellow, sparsely and irregularly glandular (glands minute), lobes setulose abaxially; peripheral florets with corollas 3.5–4.4 mm long, limbs 1–3(–4) mm diam, longest pappus scales 0.13–0.71× corolla length; inner florets with corollas 3.9–5 mm long, limbs 0.75–1.75 mm diam, longest pappus scales (0.5–) 0.64–0.9× corolla length. **Cypselae** ca. 3–5.5 mm long, sparsely strigose to ± glabrate, hairs white, ascending, mostly non-overlapping. **Pappus** uniseriate, of 4 white-membranous, generally unequal, apically erose, often obtuse or abruptly acute scales, longest 2.3–4.3 mm long, linear to lanceolate or oblanceolate. **Chromosome number** $2n=5_{II}$ (D. W. Kyhos, Univ. of California, Davis, personal communication; Turner et al. 1973; Pinkava and Keil 1977).

Paratypes

MEXICO, Baja California, Central Desert, 10.6 km NE of junction with Federal Highway 1 along Federal Highway 5, toward Bahia San Luis Gonzaga, 17 May 1991, *B.G. Baldwin 758, S.J. Bainbridge, S.N. Martens* (UC); immediately N of Laguna Chapala, 17 May 1991, *B.G. Baldwin 761, S.J. Bainbridge, S.N. Martens* (UC); Cataviña Boulder Field, 0.3 km SW of Federal Highway 1 on road intersecting the highway at 9.5 km N of Cataviña, 18 May 1991, *B.G. Baldwin 765, S.J. Bainbridge, S.N. Martens* (UC); several miles N of Catavina and Santa Ynes along Mexico Highway 1, 31 March 2005, *S.J. De Groot s.n., J.M. Porter, L. Machen, J. Anderson* (RSA); vicinity of Laguna La Guija (S of Cataviña and NW of Laguna Chapala), 20 April 2017, *J. Rebman 33054 & 33068, J. LaGrange, D. Applegate* (SD, UC); 18 miles S of Bahia San Luis Gonzaga, 24 March 1970, *A.M. Powell & B.L. Turner 1763* (TEX); Route 1, ca. 54 miles S of El Rosario, 25 May 1974, *D.J. Pinkava P12186, Reeves, Hensel, McGill* (ASU); along Mexico Highway 1, 4.5 miles NW of El Crucero, 23 March 1988, *J.L. Reveal 6721, C.R. Broome, R.K. Solomon, S.N. Saylor* (UC).

Chaenactis kyhosii can be distinguished from *C. glabriuscula* s. l. and other yellow-flowered members of *Chaenactis* (i.e., *C. nevii* A.Gray, endemic to Oregon, and an undescribed lineage from northern Baja California, to be published elsewhere with D. W. Kyhos) by the following combination of characteristics: non-glandular hairs sparse or lacking, main stem branches diverging at or near base, most leaves basal and proximal, leaf blades generally 1-pinnate with filiform segments or blades entire and filiform, peduncles and involucres strongly glandular, marginal corollas only slightly enlarged, cypselae sparsely strigose to ± glabrate with hairs white and mostly non-overlapping, and a

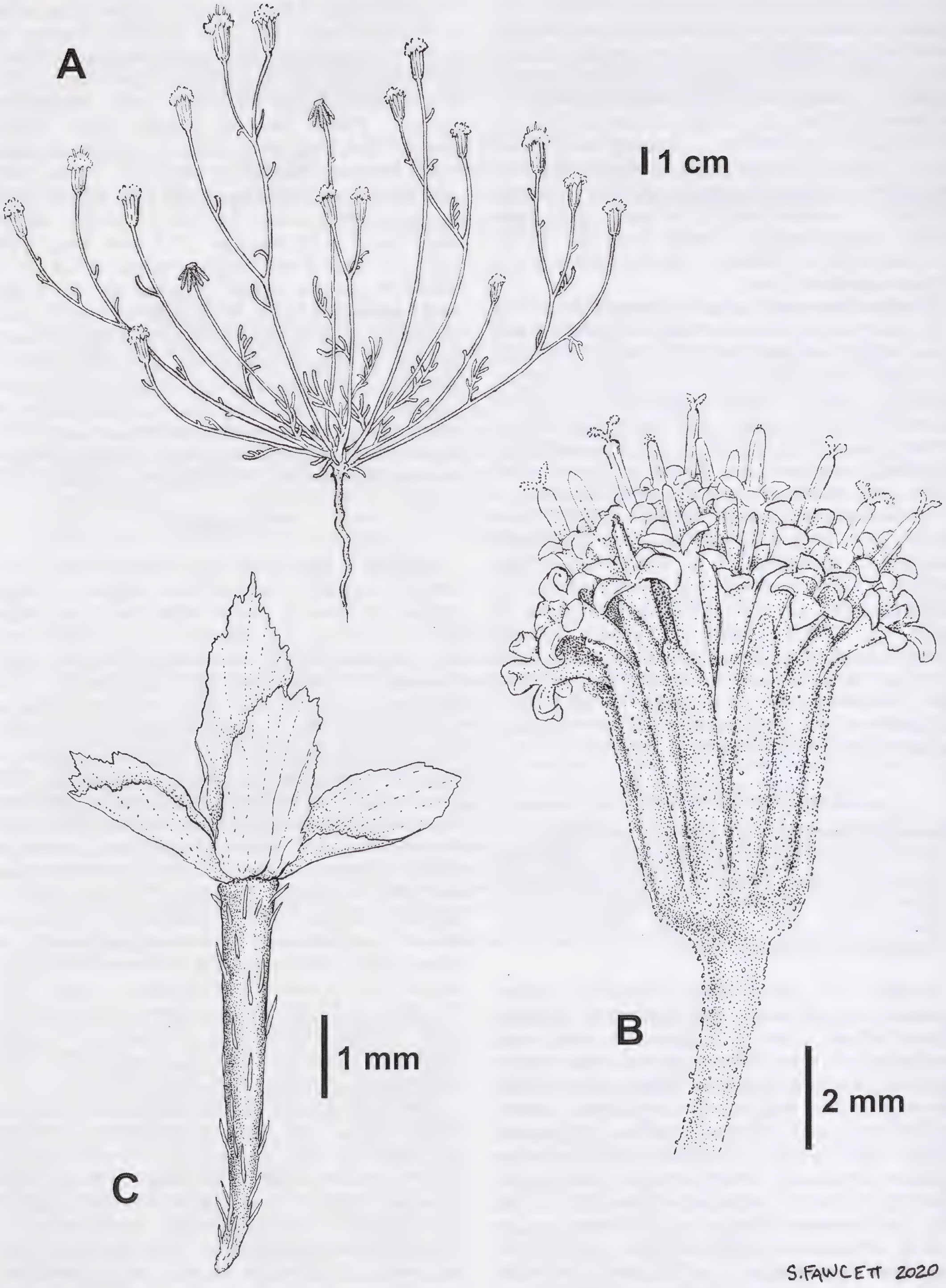

FIG. 1. *Chaenactis kyhosii*. A. Habit. B. Head and distal peduncle. C. Fruit of inner floret with pappus.

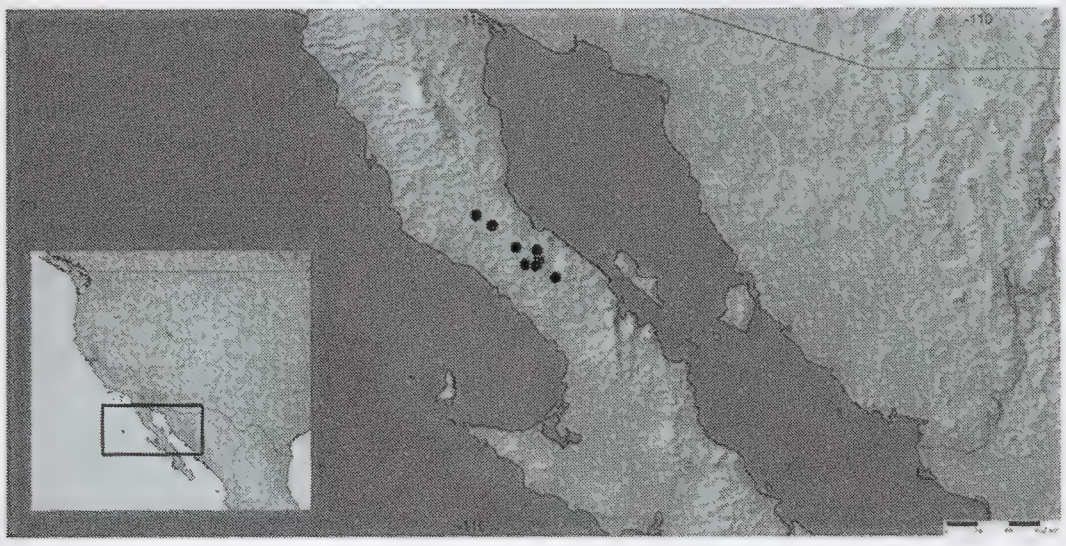

FIG. 2. Geographic distribution of *Chaenactis kyhosii* based on vouchered collections, i.e., the type and paratypes. All known occurrences are within the Central Desert of Baja California. Map produced using Simplemappr (simplemappr.net).

pappus of one series of four well-developed, generally unequal, often obtuse scales, in addition to having five pairs of chromosomes. *Chaenactis kyhosii* is especially similar to some populations of *C. glabriuscula* s. l. from the southwestern California Floristic Province and desert periphery in Baja California. There, individuals of *C. glabriuscula* s. l. that approach *C. kyhosii* in vegetative characteristics generally have more distinctly radiant and sometimes larger heads, with more expansive limbs of marginal corollas, often longer and more gradually tapered (frequently acute) pappus scales of inner florets, and sometimes tawny, rather than white, cypselae hairs. *Chaenactis kyhosii* is easily distinguished from sometimes co-occurring *C. lacera* Greene by its entire to generally 1-pinnate (rather than 2–3-pinnate) leaves, bright yellow (rather than white to pinkish or lavender) corollas, and uniseriate (rather than multiseriate) pappus of 4 (rather than 10+) scales. Based on molecular phylogenetic evidence (Baldwin and Kyhos unpublished data), *C. kyhosii* is more closely related to the white-flowered *C. fremontii*, also with $2n = 5_{II}$, and southern lineages of *C. glabriuscula* s. l., than to northern lineages of *C. glabriuscula* s. l.

Chaenactis kyhosii is known from the Central Desert of Baja California, in sandy to rocky open sites, including vernal lake margins, granitic boulder fields, and rhyolitic slopes, from ca. 500 to 700 m elev. (Fig. 2). Flowering has been documented from March to May. Woody associates include *Ambrosia chenopodifolia* (Benth.) W.W.Payne, *A. dumosa* (A.Gray) W.W.Payne, *A. pumila* (Nutt.) A.Gray, *Atriplex polycarpa* (Torr.) S.Watson, *Bursera microphylla* A.Gray, *Encelia farinosa* A.Gray ex Torr., *Eriogonum fasciculatum* Benth., *Fouquieria columnaris* (Kellogg) Kellogg ex Curran, *Larrea tridentata* (DC.) Coville, *Lycium californicum* Nutt. ex A.Gray, *Pachycereus pringlei* (S.Watson) Britton & Rose, and *Prosopis glandulosa* Torr. var. *torreyana* (L.D.Benson) M.C. Johnst. Herbaceous associates include *Amblyopappus pusillus* Hook. & Arn., *Caulanthus lasiophyllus* (Hook. & Arn.) Payson, *Chaenactis lacera*, *Chorizanthe brevicornu* Torr., *Erodium cicutarium* (L.) L'Hér. ex Alton (naturalized), *Eulobus californicus* Nutt. ex Torr. & A.Gray, *Malacothrix coulteri* Harv. & A.Gray, and *Stipa speciosa* Trin. & Rupr.

ETYMOLOGY

The species epithet honors Donald W. Kyhos, Professor Emeritus of Plant Biology at the University of California, Davis. He first recognized the species to be distinct from *C. glabriuscula* s. l. and found it to be chromosomally differentiated from other members of *Chaenactis* sect. *Chaenactis*, in addition to his other contributions toward understanding the evolution and diversity of *Chaenactis* more generally.

CONSERVATION STATUS

Chaenactis kyhosii is known from a limited geographic area in the Central Desert of Baja California. The narrow known distribution of *C. kyhosii* warrants conservation concern and further efforts to document the status and extent of its occurrences. Expected variation in germination and survival across years, with fluctuations in desert climate, may necessitate repeated surveying to accurately characterize the distribution and abundance of these spring-flowering annuals.

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A NEW SPECIES OF *CRYPTANTHA* RESTRICTED TO DUNES IN NORTHWESTERN BAJA CALIFORNIA, MEXICO

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ABSTRACT

Cryptantha arenophila Rebman & M.G.Simpson (Boraginaceae) is described as new. This species is restricted to sandy dunes near San Quintín, Baja California, Mexico and adjacent coastal regions. It is similar to the more common *Cryptantha patula* Greene in stem vestiture, calyx morphology, and inflorescence morphology. *Cryptantha arenophila* differs from that species in having significantly larger corolla limbs and narrowly oblong to narrowly elliptic leaves with obtuse-rounded leaf apices, as opposed to linear to narrowly lanceolate leaves with acute to obtuse leaf apices in *C. patula*. In addition, nutlets of *C. arenophila* tend to have more numerous and shorter tubercles, while those of *C. patula* have tubercles that are less dense and larger, although variation in this species needs further investigation. The dune habitats where the type locality of *C. arenophila* occurs are currently under severe impacts from animal grazing and off-road traffic, necessitating the conservation of these regions.

Key Words: Baja California, Boraginaceae, conservation, *Cryptantha arenophila*, *Cryptantha patula*, dunes, taxonomy.

Cryptantha is a genus of annual or (only in South America) perennial herbs of the family Boraginaceae. Based on molecular phylogenetic studies (Hasenstab-Lehman and Simpson 2012; Simpson et al. 2017; Mabry and Simpson 2018), *Cryptantha* is currently recognized with about 103 species and 118 minimum-ranked taxa, having been split from the genera *Eremocarya, Greeneocharis*, *Johnstonella,* and *Oreocarya* (see Hasenstab-Lehman and Simpson 2012 for a key to genera and Amsinckiinae Working Group 2021 for updated taxonomy). These five genera were previously grouped together within *Cryptantha* s. l., by a feature of their fruits ("nutlets"), all having a characteristic ventral (adaxial) groove running the length of the nutlet, corresponding largely to the scar of attachment to the central gynobase. Species and infraspecies of *Cryptantha* have been distinguished in large part by the size, shape, number per fruit, sculpturing, and ventral groove morphology of the nutlets, but also by plant duration, leaf position, leaf morphology, vestiture, calyx morphology, and corolla size, shape, and color (see Simpson and Hasenstab 2009; Kelley et al. 2012).

In reviewing the *Cryptantha* species of Baja California and Baja California Sur, Mexico, we discovered specimens with unusually wide leaves and large flowers, these confined to sandy dune habitats in northwestern Baja California. A subsequent collecting trip in April 2017 confirmed this. Members of these populations are similar to *Cryptantha patula* Greene (Greene 1889), resembling that species in having decumbent to ascending branches with long cymule units and an elongate peduncle subtended by leaf-like bracts, with some bracts subtending the lowermost flowers. However, *C. patula* has much narrower leaves, smaller flowers, and a different nutlet morphology (see Results, Discussion). We believe this new entity is different enough to warrant naming it as a new species. Here we name and describe the species and provide results of a quantitative analysis corroborating its distinctiveness, utilizing a taxonomic (morphologic) concept (Cronquist 1978, 1988). We cite information on vital conservation needs for this new species, review some taxonomic challenges for future work in this complex, and provide a taxonomic key for its identification.

TAXONOMIC TREATMENT

Cryptantha arenophila Rebman & M.G.Simpson, *sp. nov.*—Type: MEXICO. **Baja California**. *J. Rebman 33048*, with M. G. Simpson, M. Mulligan, and S. Vanderplank, 19 April 2017 (holotype: **SD**278625; isotypes: **BCMEX**, **MEXU**, **RSA**, **SBBG**, **SDSU**, **UC**), Mpio. Ensenada, El Socorro Dunes: south of San Quintín and just north of Arroyo Socorro, dune fields above the ocean, prostrate annual, flowers white, common, note heteromorphic sepals, dune vegetation, with *Acmispon distichus* (Greene) Brouillet, *Nemacaulis denudata* Nutt., *Brassica tournefortii* Gouan, *Eulobus crassifolius* (Greene) W.L.Wagner & Hoch, and *Cryptantha* sp., 30.32735°N, 115.82779°W, 30 m elevation.

Paratypes. (Note: georeference coordinates and elevations indicated with an asterisk were estimated

from label data.) MEXICO, **Baja California**. *F. Casillas 214* (**SD**267039), 30 March 2010, Mpio. San Quintín, La Chorera, coastal sand dunes, 30.4542°N, 116.033°W, 6 meters elevation*; *P. Flanagan s.n.* (**SD**132560), 23 April 1989, San Quintín, 30.55775°N, 115.93919°W*, 28 meters elevation*; *J. Henrickson 4460* (**SD**80913), 25 March 1970, 2 miles W of Colonia Guerrero in sand dunes near Colonia Mormona, fls white, with *Oenothera, Astragalus*, *Ephedra, Abronia, Carpobrotus*, etc., 30.71896°N, 116.03322°W*, 3 meters elevation; *N. Jensen 691* (**SD**253407), 18 March 2014, San Quintin region, El Socorro Dunes, WGS 1984: 30.327185°N, 115.82766°W, 35.9 meters elevation, coastal dunes, stable back side of sand dunes dominated by *Helianthus niveus* (Benth.) Brandegee, slope=slight, aspect=east, associates: *Schismus* sp., *Abronia umbellata* Lam., *Oenothera wigginsii* W.M.Klein, *Helianthus niveus, Ephedra* sp., *Euphorbia* sp., herb, annual, flowering, flower color white, infrequent; *A. Johnson 128* (**SD**116684), 25 March 1973, Laguna Mormona, lee slope of dunes, atypical in broad leaves, large corollas, 30.66067°N, 116.0333°W*, 5 meters elevation; *P. W. Rundel 2106* (**IRVC**18157, **SDSU**22355), 15 March 1973, San Quintin, Colina del Sudoeste, sand dunes, 30.44237°N, 116.029821°W*, 28 meters elevation*.

Description (Figs. 1–3). [Note: Leaf measurements are ranges of averages from examined specimens, with minimum and maximum values in parentheses.] **Plants** annual with single taproot, aerial stems to 45 cm long. **Stems** ascending to decumbent, branched, especially near base (Fig. 1A,B), aerial stem vestiture antrorse-strigose (Fig. 1D), interspersed with minutely pustulate, spreading hirsute to hispid trichomes; older stems with more pronounced, pustulate spreading hirsute trichomes. **Leaves** (13)16–23(30.5) mm long x (2.5)2.9–4.9(5.2) mm wide, length:width ratio (3.6)3.9–7.2(8.2), narrowly oblong to narrowly elliptic, apically obtuse-rounded (Fig. 1A–C), both surfaces with whitish, appressed to inclined hirsute, trichomes, these pustulate, with basal ring of cells, midrib sunken adaxially, raised abaxially, leaves reduced distally. **Inflorescence** cymules mostly solitary (Fig. 1A), arising from lower axes, peduncles 5–27 cm long, cymules circinate, with deciduous, basal inflorescence bracts, 15-25-flowered, elongate in fruit, up to 10 cm long from lowermost to uppermost flowers, lowest fruits not touching one another, 3–5(9) mm apart, isolated flowers often found at junction of inflorescence axes, flower bracts mostly absent, occasionally present near base of cymule (Fig. 1A), bracts similar to but smaller than vegetative leaves. **Flowers** subsessile, pedicel ≤0.5 mm. **Calyx** horizontal to inclined, lance-ovoid at maturity, 2.5–3.5 mm at anthesis, (4)5–7 mm in fruit; sepals distinct, heteromorphic by size, with 1–2 typically longer, linear to narrowly lanceolate, apically rounded, erect with tip slightly recurved when dry, midrib thickened adaxially and abaxially, margins densely ascending fine-hirsute, adaxial surface glabrous below, appressed short hirsute near apex, abaxial surface appressed to spreading hirsute marginally, with ascending to horizontal, pustulate, inflated, hispid trichomes along thickened midrib, white throughout or white with yellowish tip (Fig. 2A,B). **Corolla** white, rotate, tube about equal to calyx, limb 5–6 mm in diameter, fornices yellow, rarely white (Fig. 1C). **Gynobase** ca. 1/2–2/3 height of nutlet; style tip/stigma extending to or very slightly beyond mature nutlets (Fig. 2B). **Ovules** 4, sometimes abortive. **Nutlets** (1)2–4 (Fig. 2A), 1.8–2.0 mm long, homomorphic, brownish to grayish, often dark mottled, lance-ovate, base truncate to slightly rounded, margins rounded, apex acuminate, dorsal surface convex, spinal ridge absent, ventral surface flat at base, both surfaces finely and densely papillate and low-rounded tuberculate with ca. 14–20 tubercles within a 0.1 mm high transverse band of the dorsal face at the widest region (Fig. 3A–D), attachment scar edges abutted or slightly separated entire length, not raised, gapped at base forming a small, triangular areole, bi-forked below (Fig. 3A).

Diagnosis. *Cryptantha arenophila* is similar to *C. patula* in having both appressed and spreading stem trichomes and mostly solitary, often basally bracteate cymules, differing from the latter in having relatively wide (ca. 3–5 mm) leaves with a length:width ratio <8, relatively wide (5–6 mm) corolla limbs, and nutlets with smaller, more numerous tubercles.

Distribution, Habitat, and Endemism. *Cryptantha arenophila* is endemic to a limited region of northwest Baja California, Mexico (Fig. 4A,B), distributed on coastal sand dunes in the vicinity of San Quintín and adjacent coastal regions, from the mouth of the Santo Domingo River near Colonia Vicente Guerrero in the north, south to the El Socorro dune field; <40 meters elevation.

Phenology. Based on data from available specimens, *Cryptantha arenophila* appears to flower and fruit from March to May, the fruits likely persisting into the early summer.

Etymology. Latin *arenos*, sand, + *phila*, from *phileo*, to love, in reference to its typical occurrence on sand dunes (pronounced *a-re-nó-phi-la*). Note that *Cryptantha arenophila* should not be confused with the similar-sounding *Cryptantha arenicola* A.Heller, which is currently recognized as a heterotypic synonym of *Cryptantha nevadensis* A.Nelson & P.B.Kennedy.

Suggested Common Name. San Quintín Dune Cryptantha.

Rejected Paratypes. We examined two herbarium specimens that had relatively wide, short leaves that were within or close to dimensions of *Cryptantha arenophila*, both of which we rejected. These are

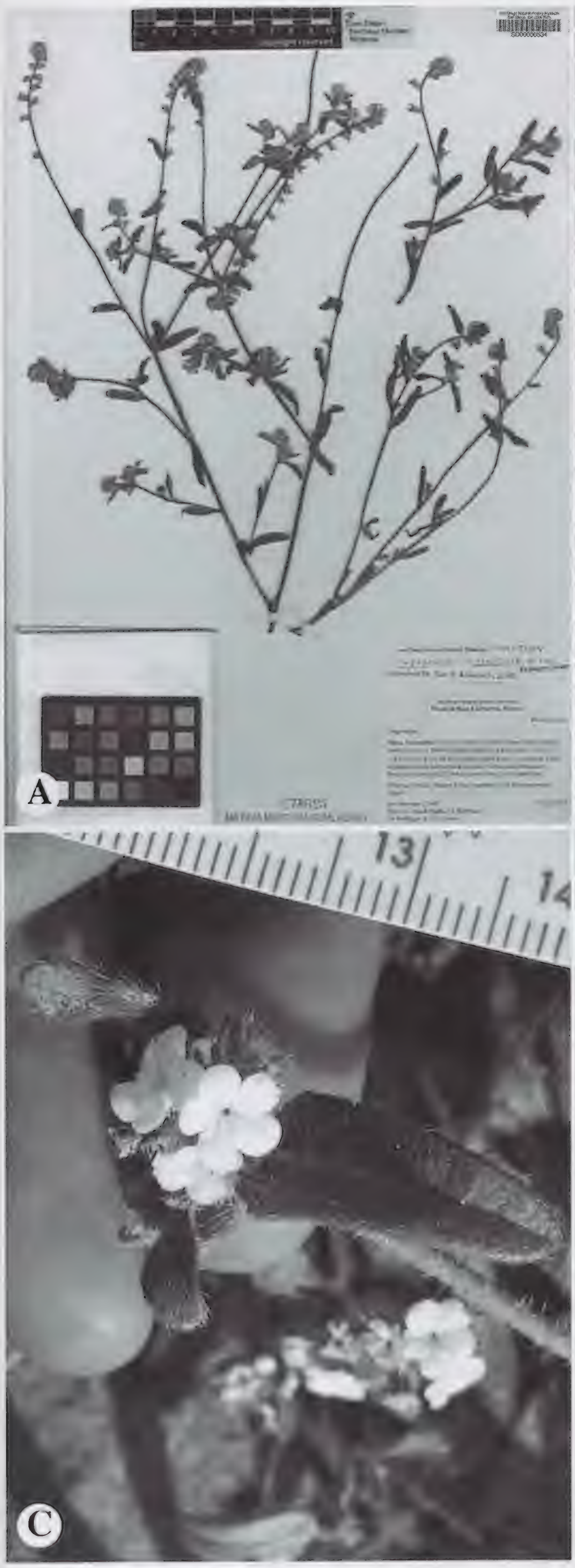

FIG. 1. *Cryptantha arenophila*. A. Holotype specimen (*Rebman 33048*, **SD**278625), showing elongate cyme units and wide leaves. B,C. Habit photographs, type population. Note typical sand dune habitat and relatively large leaves and corollas. D. Stem close-up, just below cymule, showing both antrorse-appressed and spreading-hirsute trichomes.

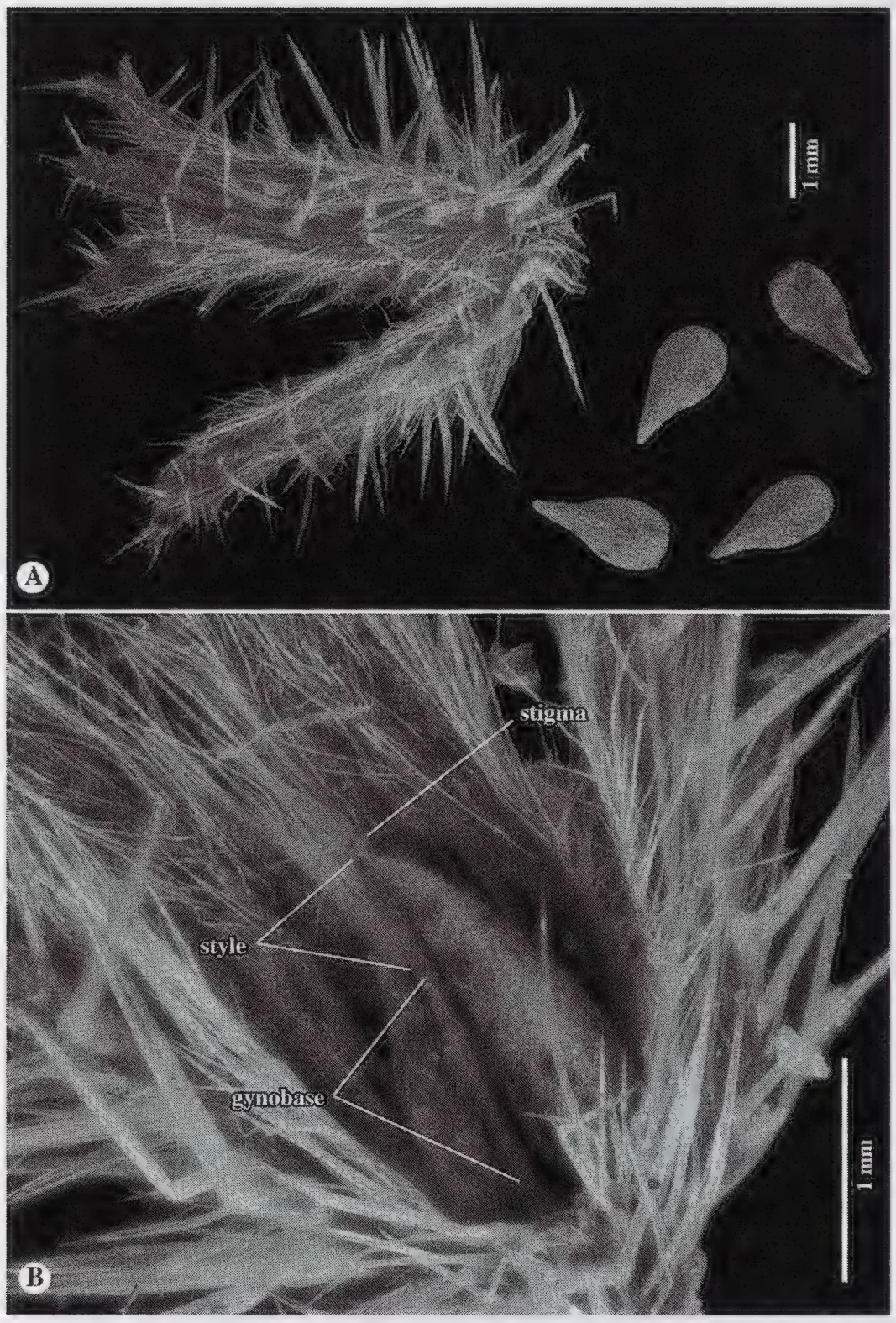

FIG. 2. Fruits of *Cryptantha arenophila*, from type material (*Rebman 33048*). A. Fruit with 4 nutlets removed. Note sepals with coarse, hispid trichomes along adaxial midrib and ascending hirsute trichomes along margin and outer surface, typical of many *Cryptantha* species. B. Fruit close-up, showing mature nutlet attached to gynobase, one nutlet (at left) abortive, one removed (not shown). Note style tip/stigma extending just beyond nutlet apex.

listed below with the reasons for not considering them representatives of this new species.

R. Moran 21837, 21 April 1975 (**SD**91282), Mexico, Baja California, ca. 5 miles northwest of San Quintín, common on dunes atop low beach bluffs, 30°33′N, 116°02′W, 20 meters. This specimen resembles *C. arenophila* in having wider leaves, elongate, basally bracted cymes, and relatively large corollas. It also occurs on dunes within the range of *C. arenophila*. We reject it because the nutlets have relatively large tubercles and a longer style length (extending ca. 0.5 mm above the nutlets), similar to that of mainland *C. patula* s. l.

J. Henrickson 19346, 19 March 1983 (**RSA**660863), Mexico, Baja California, ca. 55 air miles SE of Bajia [sic] San Luis Gonzaga at ruins of Mina Desengaño, in granite area with ocotillo [*Fouquieria splendens* Engelm. subsp. *splendens*], Boojum tree [*Fouquieria columnaris* (Kellogg) Curran], *Ambrosia dumosa* (A.Gray) W.W.Payne, *Yucca valida* Brandegee, *Ephedra, Lycium, Atriplex, Agave, Viscainoa*, etc., near 29°07′N, 114°05′W, 300 ft.

Although this specimen has relatively wide leaves, the nutlets are coarsely tuberculate, the tubercles somewhat conical and sharp-pointed, quite different from those of *C. arenophila* and a typical *C. patula*. Also, although this specimen does have some apparent elongate "solitary" cyme units as in *C. arenophila* and forms of *C. patula*, it also has some that are trifurcate, resembling *C. intermedia* (A.Gray) Greene. The corolla limb width (maximum 3 mm) of this specimen is more typical of *C. patula*. Finally, this specimen is well out of range of *C. arenophila*, at about 280 km (175 miles) southeast of the nearest *C. arenophila* population and in the middle of the peninsula, not in coastal habitats.

MATERIALS AND METHODS

Field collections and photographic documentation of this large-leaved *Cryptantha* were made in April 2017, the collections serving as type material. Herbarium specimens of these and of *C. patula* were obtained and studied from the following herbaria: University of California Irvine (**IRVC**), San Diego Natural History Museum (**SD**), San Diego State University (**SDSU**), Santa Barbara Botanic Garden (**SBBG**), and the Smithsonian Institution (**US**). Additional online specimen images of related taxa were also examined from the Harvard University Herbarium (**GH**) and the California Botanic Garden (**RSA**) (acronyms after Thiers, continuously updated). A total of six specimens of *C. arenophila* (all but one known) and 16 collections of *C. patula* were measured (Appendix 1). Photomicrographs of selected parts of *C. arenophila* and of *C. patula* were taken with a Visionary Digital Imaging System using a Canon EOS 5D Mk II DSLR with an Infinity model K2 tube lens fitted with a CF-4 adapter. Three to five of the lowermost, largest leaves were measured for length and width, and the mean length, width, and length:width ratio per specimen were calculated. The corolla limb width was measured, the maximum value used because of corolla shrinkage in dried specimens. For a limited number of specimens having high resolution photomicrographs, quantification of tubercle density on the nutlet dorsal face was approximated by tabulating the number of tubercles occurring within a 0.1 mm band (whole tubercles or those >50% within the band) at the widest transverse axis of the nutlet. Nutlet tubercle size was not quantified because this feature could not be accurately measured from the images available. The software ImageJ (Scheinder et al. 2012) was used to quantify these metrics. Box plots showing the median and four quartiles of distribution were prepared of the two taxa for: 1) median leaf width (mm); 2) median leaf length:width ratio; 3) maximum (within a specimen) corolla limb diameter (mm); and 4) nutlet tubercle density. T-tests were performed to evaluate statistical differences ($\alpha = 0.05$ and $\alpha = 0.01$), using Microsoft Excel, version 16.44. A distribution map, using the mapping function of the Berkeley multi-

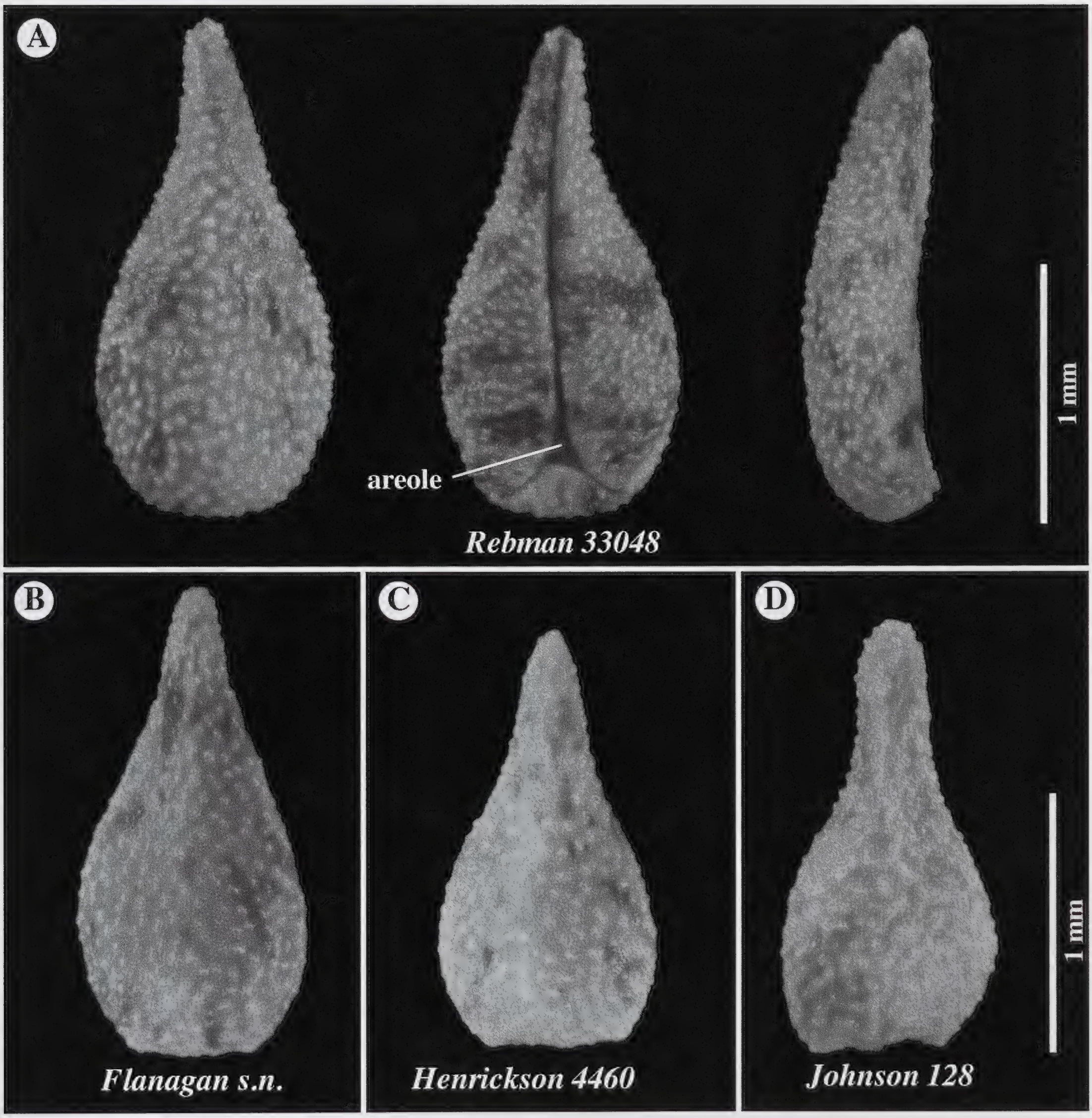

FIG. 3. Nutlet images of *Cryptantha arenophila*, showing densely papillate and low-tuberculate sculpturing. A. Type material (*Rebman 33048*) showing dorsal (left), ventral (middle), and lateral (right) views. B–D. Nutlet images of additional paratype specimens, all dorsal view: B. *Flanagan s.n.* (**SD**132560). C. *Henrickson 4460* (**SD**80913). D. *Johnson 128* (**SD**116684).

mapper tool (CCH1 2020), was prepared of all known specimens of *Cryptantha arenophila* plus specimens identified as *C. patula* from Baja Flora (2020), CCH2 (2020), and SEINet (2020).

RESULTS

The box plots and t-tests of *C. arenophila* and examined specimens identified as *C. patula* showed differences between the two taxa in median leaf width (Fig. 5A), median leaf length:width ratio (Fig. 5B), maximum corolla limb diameter (Fig. 5C), and nutlet tubercle density (Fig. 5D), all significant at $P < 0.01$. However, leaf length (boxplot not illustrated) showed considerable overlap between the two taxa, with $P > 0.05$. Measurements of type specimens ("**t**" in Fig. 5) fall within the two 25% quartiles above and below the mean in all of these features with the exception of nutlet tubercle density, in which the value of the type specimen of *C. arenophila* is in the upper quartile; this feature was unobtainable for the type of *C. patula* (Fig. 5D) because of unavailability and probable immaturity of the type material.

Qualitative observations of specimens showed that the two forms are similar in having mostly "single",

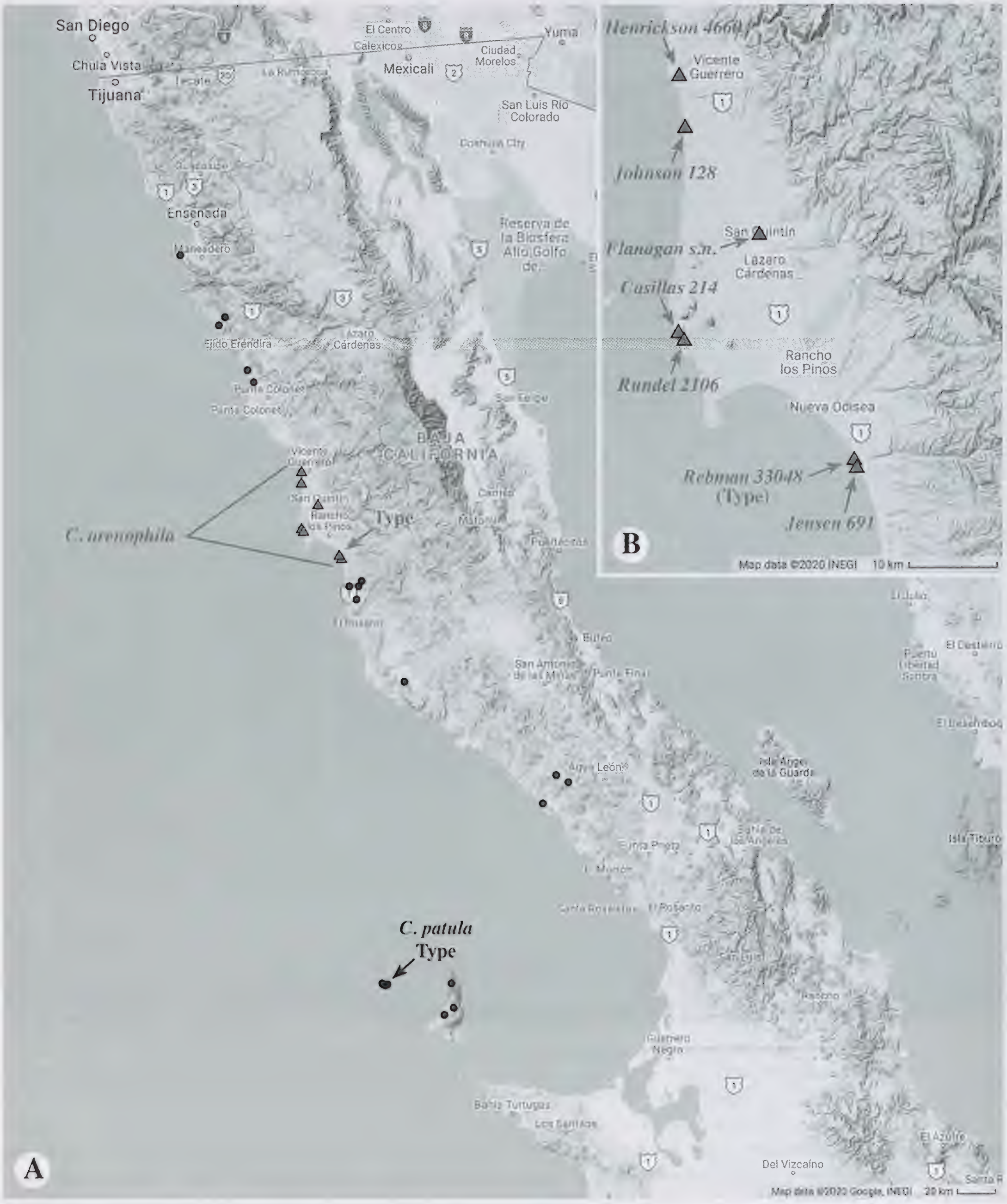

FIG. 4. Distribution of *Cryptantha arenophila* (red triangles) and specimens identified as *C. patula* s. l. (black dots), from examined and measured herbarium specimens, type localities of both species indicated; data from SEINet (2020), CCH2 (2020), and Bajaflora (2020). Inset: Magnified image of San Quintín region, showing localities of all currently known specimens of *C. arenophila*. Maps from ©Google 2020, INEGI Data.

elongate cymules, meaning that the cymules do not branch after the occurrence of basal inflorescence bracts (Figs. 1A, 6C). Our measurements of corolla limb width show that *Cryptantha arenophila* has a consistently wider maximum corolla limb width (ca. 5–6 mm limb diameter; see Fig. 1C) than *Cryptantha patula* (ca. 2.5–4 mm), quantified in Figure 5C. Nutlets of both forms were similar in being lance-ovate with a narrowly acute to acuminate apex, rounded margins, and a papillate-turberculate sculpturing (Figs. 3, 6F). However, as illustrated in Fig. 5D, nutlets of *C. arenophila* have more numerous,

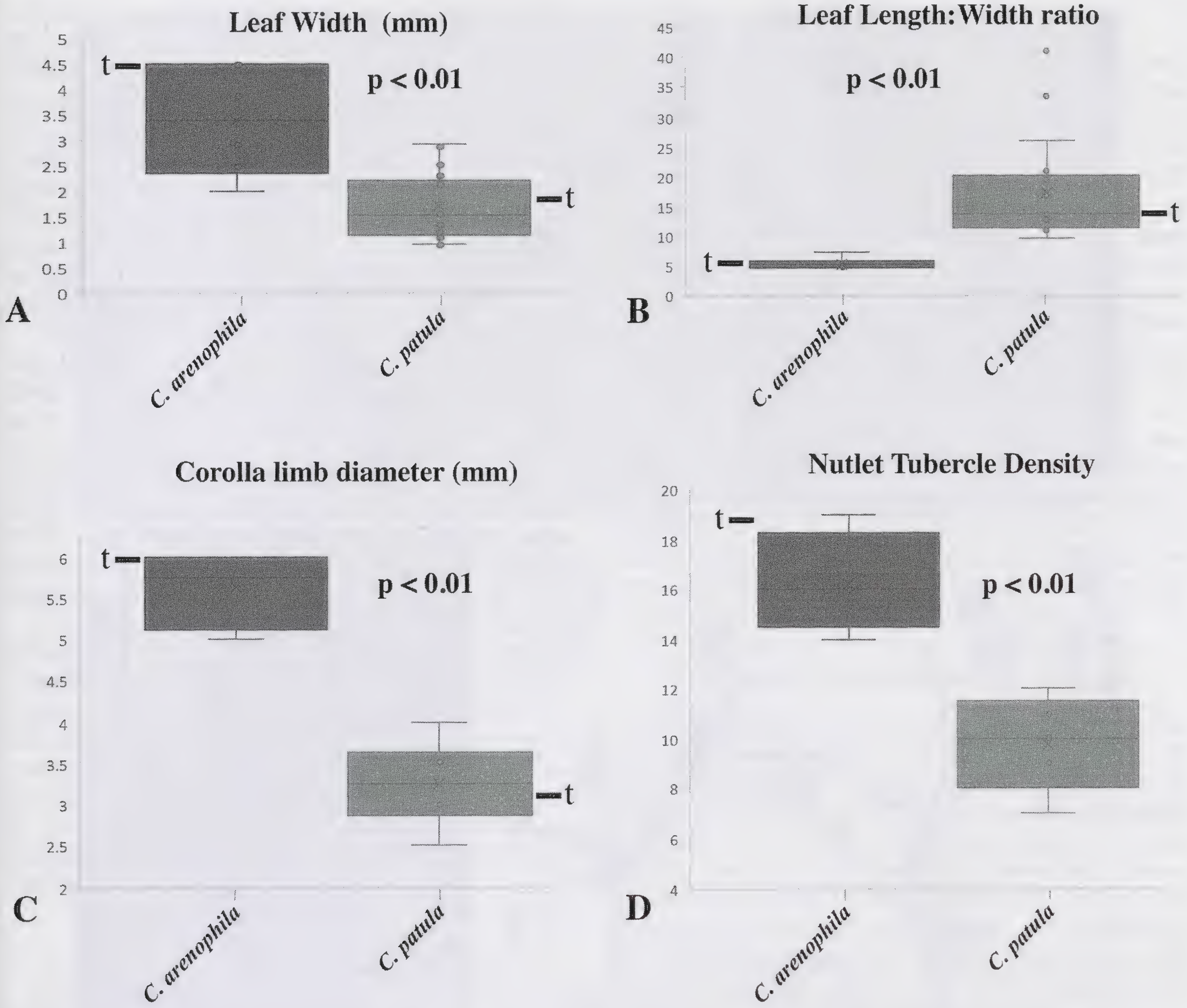

FIG. 5. Box plots comparing quantified leaf measurements of *Cryptantha arenophila* and *C. patula*. A. Leaf width (mm). B. Leaf length:width ratio. C. Maximum corolla limb diameter. D. Nutlet dorsal surface tubercle density (tubercle number within a 0.1 mm transverse band at widest point). In all cases, the two taxa are different at $P < 0.01$. Box plots show median (horizontal line), first and third quartiles (boxes above and below median), and second and fourth quartiles (vertical lines); outliers indicated by small dots. Abbreviation: **t** = values of the type specimens of the corresponding two species. Note that nutlet tubercle density was unobtainable for the type specimen of *Crypantha patula* (Fig. 5D).

smaller (shorter) tubercles (Fig. 3) than *C. patula*, which have fewer, longer, and stouter tubercles (Fig. 6F), the latter resembling those of a typical *Cryptantha intermedia* (see Amsinckiinae Working Group 2020). The relative style length of the two species was not quantified because of scarcity of specimens. However, observed specimens of *C. arenophila* have a relatively shorter style, extending to or just beyond (ca. 0.1 mm) the nutlet apices of mature fruits (Fig. 2B). Styles of *C. patula* were observed to be longer, extending to about 0.5 mm above the nutlet apices (Fig. 6D).

DISCUSSION

We chose to recognize this new entity at the species level because of its discrete leaf morphology, relatively large corolla size, distinctive nutlet sculpuring, habitat specificity, and limited geographic range. We did not consider an infraspecific rank to other *Cryptantha* taxa because its relationship to other taxa is unclear. *Cryptantha arenophila* is similar to *C. patula* in stem vestiture (both species having both appressed and spreading trichomes; Figs. 1D, 6E), calyx morphology (both species having distinct, linear, apically rounded, and heteromorphic sepals), and inflorescence morphology (both species with what are described as "solitary" cymules [also termed "spikelets" in the literature]) (Figs. 1A, 6C). As seen from quantitative leaf measurements, *Cryptantha patula* differs in having considerably narrower leaves, being linear to narrowly lanceolate (see Fig. 6A, B for image of holotype specimen of *C. patula*; note that the holotype is a rather immature specimen). In addition to leaf morphological differences, *Cryptantha arenophila* has a consistently wider corolla limb

FIG. 6. *Cryptantha patula* images. A,B. Holotype specimen, *C.F. Pond 21*, Feb. 1889, Mexico: Baja California, San Benito Islands (US47037). Note narrow leaves, the type material somewhat immature. C–F. Exemplar of *C. patula* from San Benito Island, the type locality: *S. A. Junak 5308*, 15 March 1993 (**SBBG**108802). C. Herbarium sheet, showing elongate, linear to lanceolate leaves and bracts at base of cymules or lower flowers. D. Fruit close-up, showing relatively elongate style. E. Stem, just below cymule, showing antrorse-appressed and spreading-hirsute trichomes, similar to *C. arenophila*. F. Nutlet in dorsal, ventral, and lateral views, showing papillate-tuberculate sculpturing, with tubercles longer and less dense than *C. arenophila*.

width (5–6 mm limb diameter; Fig. 1C, 5C). In the Protologue for *Cryptantha patula* (Greene 1889), the corolla is cited as "rather large" (p. 266), with Johnston (1925) describing the corolla limb width of this species as "1.5–3 mm long" (p. 62). Our examination of several specimens of *Cryptantha patula* yielded a maximum corolla limb width range of 2.5–4 mm, confirming that it is smaller than *C. arenophila*. Finally, the differences in nutlet sculpturing, in terms of density and size of tubercles, of the two species is diagnostic.

The relatively wide leaves of *Cryptantha arenophila* may possibly be an adaptation to its occurrence in sandy dunes, the larger leaves able to withstand or resist being covered by shifting sands. However, we note the occurrence of a narrow-leaved specimen tentatively identified by us as *Cryptantha* cf. *patula* in sands at the base of the dune near the type specimen of *C. arenophila*, which indicates that the larger leaves of *C. arenophila* are not the result of environmental plasticity.

Cryptantha arenophila is much more limited in distribution than *C. patula* s. l., the latter known to occur from near Santo Tomás to the vicinity of Punta Canoas and on San Benito and Cedros Islands in Baja California (Fig. 4). *Cryptantha arenophila* is restricted to the Coastal Succulent Scrub (maritime succulent scrub) ecoregion, whereas *C. patula* occurs in that region plus the western Central Desert, Vizcaino Desert, and Pacific Islands regions (Rebman et al. 2016).

Cryptantha patula

Cryptantha patula was named and described by Greene (1889). The type specimen was not indicated by Greene. Johnston (1925) indicated one collection in his description of the species: "San Benito Island, 1897, Brandegee (**G**, **UC**)." Thus, the type of *C. patula* is thought to be (Lieut.) *C. F. Pond 21* (or *C. F. Pond, s.n.*), Feb. 1889, Mexico, Baja California, San Benito Island, holotype: **US**47037; isotypes: **GH**00096299, **GH**00273561, **NDG**01388.

What has in the past been identified as *Cryptantha patula* occurs on the mainland and on Cedros, San Benito, and San Martin islands of Baja California, Mexico (Baja Flora 2020; Fig. 4). Specimens consistently have stems with both appressed and spreading trichomes, leaves linear to lanceolate in shape, and solitary inflorescence cymules. Most specimens observed also have generally four nutlets that are lance-ovate, narrowly acute to acuminate, and have a papillate, long-tuberculate sculpturing. However, in our study of *Cryptantha patula* specimens, we note some variation in that species, as treated in the broad sense. A thorough investigation of *Cryptantha patula* is beyond the scope of this study, but we point out that this species (or complex) is worthy of a future study, both morphological and molecular.

Cryptantha quentinensis

A taxon worth mentioning is *Cryptantha quentinensis* J.F.Macbride (1918). This named species was collected at San Quintín (spelled "quentin" in the epithet), Baja California in 1889 (*Palmer 695*, holotype **GH**00096300), the general region of *C. arenophila*. Our examination of the imaged holotype specimen of this taxon confirms what others have said (e.g., Johnston 1925), that *C. quentinensis* should be treated as a synonym of *Cryptantha intermedia,* and we believe of *C. intermedia* var. *intermedia,* given its stem pubescence. Like the latter, *C. quentinensis* has mostly trifurcate cymules. Interestingly, *C. quentinensis* appears to have stem trichomes that are (from the online image) predominantly appressed-strigose in orientation, with few spreading hirsute trichomes, a vestiture that we have found in a limited number of *Cryptantha intermedia*. In any case, despite its name and type locality, we are convinced that *C. quentinensis* is neither *C. arenophila* nor *C. patula*.

Endemism and Conservation Needs

Cryptantha arenophila is endemic to sandy dune habitats in a small, mostly coastal region of northwestern Baja California and quite restricted in range (Fig. 4). We are aware of two other localized endemic species that are also concentrated in this region, *Astragalus anemophilus* Greene and *Oenothera wigginsii* W.M.Klein, with the latter also occurring sporadically in a couple of populations further south. Given their similar distribution and microhabitat selection, it is possible that these three species had a common geological origin.

The type locality of *Cryptantha arenophila* (exemplified by *Jensen 691* and *Rebman 33048*) in the high sandy dunes of Socorro just south of San Quintín, Baja California, Mexico (Fig. 4B), is currently under severe habitat degradation (Clark et al. 2008; Harper et al. 2011). The San Quintin region has extensive and continuing agricultural and urban development. The dune habitats where *C. arenophila* occurs specifically are being degraded due to unrestricted livestock (cattle and goat) grazing and off-road vehicular activity and recreation. Plus, the introduction and spread of various invasive non-native plant species, such as *Brassica tournefortii* Gouan, *Carpobrotus edulis* (L.) N.E.Br., *Mesembryanthemum crystallinum* L., and *Schismus barbatus* (L.) Thell. are negatively impacting the dune vegetation.

The *Flanagan s .n.* paratype, cited as occurring in "San Quintín", is likely extirpated. Although the other, coastal populations of *C. arenophila* may be less impacted than these, we believe the protection status of the species should be high, equivalent to that of the California Native Plant Society (CNPS 2020) Inventory ranking of 1B.1 (locally rare, threatened, or endangered).

Future Taxonomic Work

The phylogenetic placements of *Cryptantha arenophila* and *C. patula* are currently unknown, as no specimens of either have been included in molecular analyses to date (Hasenstab-Lehman and Simpson 2012; Simpson et al. 2017; Mabry and Simpson 2018). We believe that this complex of species is in need of detailed morphometric and phylogenetic studies, the latter using molecular markers showing variation at the population level. The relationships of *C. arenophila* both to *C. patula* s. l. and to the varieties of *C. intermedia* will be quite interesting to elucidate. And, as pointed out, *C. patula* shows more variation in some features (e.g., calyx pubescence and nutlet morphology) than previously realized. In fact, *Cryptantha* specimens from San Martin Island, just to the west of San Quintin, somewhat resemble *C. patula*, but exhibit a nutlet morphology closer to *C. arenophila* and are rather distinct in having linear to thread-like leaves and an erect growth habit, and may represent yet another undescribed taxon. We suspect there may be cryptic taxa (Bowdler 2010) lurking in the populations that have been lumped as *C. patula*.

Key to *Cryptantha*, including *C. arenophila*

The following key, modified from Kelley et al. (2012) and Kelley and Simpson (in press) can be used to identify *Cryptantha arenophila*, and to distinguish that species from *C. patula* s.l. and *C. intermedia* var. *intermedia*, also in Baja California. Pertinent leads are in **bold**; non-applicable leads and taxa are removed.

1. Nutlet(s) all smooth or obscurely roughened
1′ Nutlets, or at least 1, variously roughened (papillate and/or tubercled)
2. At least one nutlet with margins winged or narrow, knife-like lineate-rimmed
2′ All nutlets with margins entirely rounded or angled, not winged or lineate-rimmed
3. Nutlets of 1 fruit dissimilar in size and/or sculpturing
3′ Nutlets of 1 fruit similar in size and sculpturing
4. Pedicels 2–3 mm in fruit, long-villous; calyx with single hair type, densely white, long-villous, without coarse bristly hairs
4′ Pedicels 0–1.5(–2) mm in fruit, not villous; calyx with at least 2 hair types, at least some coarse, bristly hairs present
5. Nutlets 1(–2 or 3).
5′ Nutlets generally 4
6. Corolla inconspicuous, limb 1–2 mm
6′ Corolla conspicuous, limb 2–8 mm
7. Nutlets ovate to widely ovate/deltate (length:width ratio <2)
7′ Nutlets lance-ovate to lanceolate (length:width ratio >2)
8. Nutlet dorsal and ventral surfaces glabrous to glabrate lower half, densely tuberculate to warty upper half
8′ Nutlet dorsal surfaces tuberculate over entire surfaces
9. Stem vestiture mostly appressed, sometimes sparsely spreading soft-bristly
9′ Stem vestiture both appressed and spreading hirsute or only spreading hirsute
10. Calyx 4.5–9 mm in fruit, lobe margins tufted-spreading hairy below middle; inflorescence paired, rarely solitary or 3-numerous
10′ Calyx 4–5.5 mm in fruit, lobe margins appressed fine-hairy below middle; inflorescence solitary to 5-numerous
11′ Upper stem hairs spreading only, few to none appressed; fruiting calyx spreading to inclined relative to rachis axis
11. Upper stem hairs both appressed and spreading; fruiting calyx +/- ascending relative to rachis axis
12. At least some cymules trifurcate; nutlet tubercles relatively large, sparse; widespread in mainland of California and northwestern Baja California, Mexico ... *C. intermedia* var. *intermedia*
12′ Inflorescence cymules mostly solitary, occasionally paired or 3-merous, 1–few bracteate at base
13. Corolla limb width 2.5–4 mm; leaves linear to narrowly lanceolate, average largest, basal leaf width 1–4.2 mm, average length:width ratio 9–41; nutlet tubercles relatively large, moderately dense; northwestern and central-western Baja California, San Benito and Cedros Islands ... *Cryptantha patula* s. l.
13′ Corolla limb width 5–6 mm; leaves narrowly oblong to oblanceolate, average largest, basal leaf width 2.9–4.9 mm, average length:width ratio 4–7; nutlet tubercles small, dense; mostly sandy dunes, restricted to dunes of San Quintín and adjacent coastal areas, Baja California ... *Cryptantha arenophila*

Acknowledgments

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Appendix 1

Specimens examined for leaf width, leaf length:width ratio, and corolla limb width measurements. Specimens used for nutlet tubercle density are indicated with an asterisk. Cited are collection/collection number (italics), collection date, and herbarium accession number.

Cryptantha arenophila: *F. Casillas 214,* 30 March 2010 (**SD**267039); *P. Flanagan s.n.**, 23 April 1989 (**SD**132560); *J. Henrickson 4460**, 25 March 1970 (**SD**80913); *N. Jensen 691*, 18 March 2014 (**SD**253407); *A. Johnson 128**, 25 March 1973 (**SD**116684); *J. Rebman 33048** (**Type**), 19 April 2017 (**SD**).

Cryptantha patula: *Junak 5308**, 15 March 1993 (**SBBG**108802); *Junak 5321**, 15 March 1993 (**SBBG**108801); *Moran 17143*, 31 March 1970 (**SD**76970); *Moran 20316**, 26 March 1973 (**SD**86999); *Philbrick B73-200*, 7 March 1973 (**SBBG**46951); *Philbrick B73-200*, 7 March 1973 (**SD**171992); *Pond 21* (**Type**), Feb 1889 (**US**00112170); *Rebman 22664*, 19 March 2012 (**SDSU**20155); *Rebman 22736*, 20 March 2012 (**SDSU**20158); *Rebman 22889**, 21 March 2012 (**SD**222881); *Rebman 22931*, 22 March 2012 (**SDSU**20161, **SD**222885); *Rebman 22926*, 22 March 2012 (**SD**222886); *Rebman 22998*, 23 March 2012 (**SD**222887); *Rebman 25916*, 16 April 2013 (**SDSU**20438); *Rebman 25944*, 18 April 2013 (**SDSU**20398); *Riley 22*, 28 February 2012 (**SD**227956).

Not measured (rejected paratypes; taxonomy uncertain):

Henrickson 19346, 19 March 1983 (**RSA**660863); *Moran 21837*, 21 April 1975 (**SD**91282).

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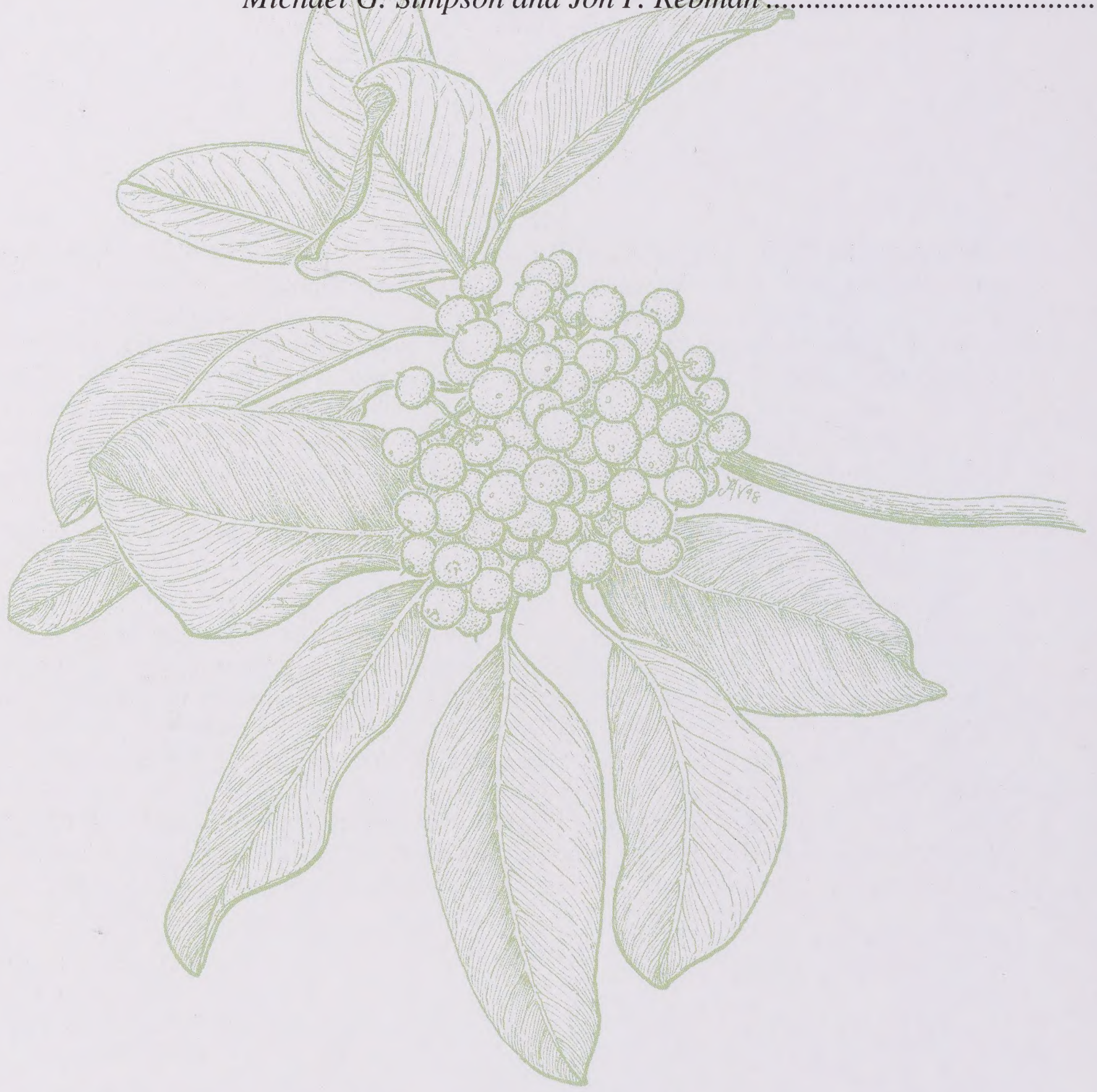

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